



ENCYCLOPEDIA  
*of* MODERN  
CORAL REEFS  
STRUCTURE, FORM AND PROCESS

*Edited by*  
*David Hopley*

 Springer

ENCYCLOPEDIA of EARTH SCIENCES SERIES



# ENCYCLOPEDIA *of* MODERN CORAL REEFS

Structure, Form and Process



# Encyclopedia of Earth Sciences Series

## ENCYCLOPEDIA OF MODERN CORAL REEFS – STRUCTURE, FORM AND PROCESS

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David Hopley is Professor Emeritus in the School of Earth and Environmental Science at James Cook University, Townsville, Queensland, Australia, where he has worked since 1965. He has an M.A. from the University of Manchester and Ph.D. from James Cook University. His initial research into Holocene sea levels and tropical landforms quickly focused on the evolution of coral reefs, reflecting the importance of the Great Barrier Reef to his home institution. Experience with coral reefs extends to many parts of the world including Australia, Barbados, India, Indonesia, Maldives, Papua New Guinea, Rodrigues and Thailand. He has authored and edited almost 200 scientific publications. Amongst numerous awards have been the J.P. Thomson silver medal from the Royal Geographical Society of Australasia (1984) and Life Membership of PACON International (1992).

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### About the Series Editor

Professor Charles W. Finkl has edited and/or contributed to more than eight volumes in the *Encyclopedia of Earth Sciences Series*. For the past 25 years, he has been the Executive Director of the Coastal Education & Research Foundation and Editor-in-Chief of the international *Journal of Coastal Research*. In addition to these duties, he is Research Professor at Florida Atlantic University in Boca Raton, Florida, USA. He is a graduate of the University of Western Australia (Perth) and previously worked for a wholly owned Australian subsidiary of the International Nickel Company of Canada (INCO). During his career, he acquired field experience in Australia, the Caribbean, South America, southwest Pacific islands, southern Africa, Western Europe, and the Pacific Northwest, Midwest, and Southeast USA.

### Founding Series Editor

Professor Rhodes W. Fairbridge (deceased) has edited more than 24 encyclopedias in the Earth Sciences Series. During his career, he has worked as a petroleum geologist in the Middle East and been a World War II intelligence officer in the southwest Pacific and led expeditions to the Sahara, Arctic Canada, Arctic Scandinavia, Brazil, and New Guinea. He was Emeritus Professor of Geology at Columbia University and was affiliated with the Goddard Institute for Space Studies.



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*edited by*

**DAVID HOPLEY**

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*Townsville*

*Australia*

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Library of Congress Control Number: 2010933113

ISBN: 978-90-481-2638-5

This publication is available also as:

Electronic publication under ISBN 978-90-481-2639-2 and

Print and electronic bundle under ISBN 978-90-481-2640-8

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Published by Springer

P.O. Box 17, 3300 AA Dordrecht, The Netherlands

*Printed on acid-free paper*

Cover photo: Houtman Abrohols, Western Australia. Photograph taken by Hironobu Kan  
(Okayama University, Japan)

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## Dedication to Rhodes Fairbridge (21st May 1914 to 8th November 2006)

A tribute to Rhodes W. Fairbridge in this Encyclopedia of Modern Coral Reefs could not be more appropriate. He was the founding editor of the *Encyclopedia of Earth Sciences Series*, launched in 1966 and continued as Series Editor and for a number of volumes, as Editor-in-Chief, until he passed away in 2006. The series consists of almost 30 volumes and reflects Rhodes' holistic knowledge of the earth, ocean and atmospheric sciences.

Although Rhodes spent his career at Columbia University in New York, he was born in Pinjarra, Western Australia. He graduated with degrees in geology from Queens University, Canada and Oxford University U.K. before receiving a DSc. from the University of Western Australia in 1942. During the war he served in the Royal Australian Air Force where, with friend and colleague Curt Teichert he became interested in aerial photography of coral reefs, initially from a military point of view but subsequently as an aid to interpreting the surficial features of reefs, his first study site being Low Isles on the Great Barrier Reef, the location of the 1928-29 Royal Society Expedition led by Sir Maurice Yonge.

From this time on Rhodes' research interests, to 1955 at the University of Western Australia, then at Columbia University, New York were intimately related to the topics around which this encyclopedia revolves. His interests in coastal geomorphology and especially in past sea level features were promoted by the spectacular calcarenite coastline of south-western Australia. Features of climate change are also prominent in arid climates, such as most of Western Australia, and this too became a focus of Rhodes' interests.

It is not surprising that Rhodes took a very active interest in the newly developing techniques of radiometric dating. In particular they allowed for the quantification of Quaternary events, particularly sea level change. He was the first to put together a sea level curve for the Holocene

and, although developed from different locations and not applicable to all sites, the Fairbridge sea level curve did much to promote coastal studies. This was no more so than at the 1969 Paris INQUA meeting where the gathering of the Sea Level Commission and the associated field excursion around the Atlantic coast of France saw the emergence of numerous ideas which were developed over the next few decades and applied to the many areas from where the INQUA delegates had come.

Rhodes was a scientist with extremely wide vision with a natural curiosity which saw him following up explanations across different fields of science. Sea level change led him into oceanography and climate change which he examined at a broad geological timescale. He was ahead of his time in accepting the Milankovitch theory directing his interests into the planetary sciences. When global climate change became a focus of discussion no-one was in a better position than Rhodes to put some of the initial ideas into a more reasonable context pointing out that the earth's climate has always been changing and that data was needed to evaluate human contribution to global warming. Again he was predicting the future direction of research although his conclusion that "Whatever the present trend, the last word will always be political", seems especially prognostic!

The ideas of Rhodes Fairbridge permeate through this encyclopedia which I believe is a most appropriate volume to pay tribute to his contributions to science in general and to the Earth Sciences Encyclopedia Series in particular. I am especially honoured to be able to make this dedication as Rhodes, who always retained his Australian citizenship, had a strong influence on the early part of my career. My honours and Masters theses were on the coast of North Wales and reference to Rhodes' sea level work was inevitable and even more so for my 1970 PhD. on the coast and islands of North Queensland. However, by



Field trip on the coast of northern France at the 1969 INQUA conference (left David Hopley, right Rhodes Fairbridge)

that time I had not only met Rhodes (initially when he passed through Townsville) but had spent more than 3 weeks with him on the second half of his expedition to the islands east of New Guinea (Misima, Rossell and Louisiades etc.). He had recognised that my experience with reefs (coming from the UK) was minimal and saw

this as an ideal opportunity for “field tutoring”. It certainly paved my way into reef research. Also on the expedition was Rhodes’ charming wife Dolores (then working for the Carnegie Museum) who did much to lighten what at times were some very dark days (including the edge of a tropical cyclone). This included suggesting that whilst at sea, the men of the expedition wear lap-laps!

More time was spent with Rhodes a few months later at the 1969 Paris INQUA meeting. We were also together on the field trip around the French coast from Sangatte to Les Sables d’Olonne, where I think Rhodes’ breadth of knowledge and respect from fellow Quaternary scientists really shone through. Subsequently, apart from a couple of days with Rhodes and Dolores at their Long Island home at Amagansett, contact for me unfortunately has only been through occasional sea level meetings and committees.

Rhodes Fairbridge has left many testaments by which he will be remembered. None, I believe, are more appropriate than the *Encyclopedia of Earth Sciences Series*. However, it is a privilege to have this dedication to such a prominent twentieth century ‘Man of Science’ especially in this specific encyclopedia on coral reefs.

David Hopley  
Editor-in-Chief

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## Preface

From navigational hazards in the seventeenth and eighteenth centuries to enigmatic scientific features in the nineteenth century, coral reefs over the last 100 years have not only been understood in greater detail but also have provided evidence of macroscale geological processes such as plate tectonics. Charles Darwin's 1842 book based on his 1831–1836 circum global voyage of exploration on HMS *Beagle* strongly focused the interests of science on coral reefs. Interestingly, his ideas of subsid-ing foundations were developed whilst in South America and before he had seen a coral reef in the field. However, his work promoted both supportive hypotheses and alternatives which included ideas on glacial sea-level control, antecedent platforms, and other ideas which were very much more divorced from field observation than those of Darwin himself, who, in the fourth chapter of his book develops the biological aspects of his theory and the various conditions under which corals can grow.

The ideas, together with his oft quoted wish,

that some doubly rich millionaire would take into his head to have borings made in some of the Pacific and Indian atolls, and bring home cores for slicing from a depth of 500 or 600 feet

were a forecast of the way coral reef research would travel in the twentieth century. Although many hypotheses have been applied to all scales of reefal features and processes, hypotheses testing is now expected, and with this has come the development of research tools such as survey techniques like aerial photography and satellite imagery. The first views of coral reefs from the sky opened up whole new dimensions and directly aided the field-based study of coral reefs, to the same extent that the laboratory analysis such as palaeoenvironmental reconstruction, has in more recent times.

The understanding of how small polyps can construct enormous coral reefs more than 100 km<sup>2</sup> is of central interest to earth scientists but is just as much the area of many other fields of science. The breakdown of

boundaries around the traditional fields of science is a developing theme of the twenty-first century and is no more so than in the study of coral reefs. Corals were initially thought to be plants until the work of André de Peyssonnel (1727) although it took another 24 years for the Royal Society of London to accept them as animals. Coral reefs are the largest structures on earth built by a combination of plants and animals and inevitably they have become the major focus of research for zoologists, botanists, and ecologists. It is impossible to study reefs without input of ideas from these disciplines. However, almost every facet of earth science – geology, geography, geomorphology, sedimentology, oceanography, palaeontology, tectonics, etc. – contributes to the understanding of coral reefs and is included in this encyclopedia. The purpose of the encyclopedia is to promote interdisciplinary research and to help in the communication between earth science and other disciplines by providing a window onto the approaches of earth science to coral reefs and giving other disciplines an understanding of the way corals are viewed by the earth science community. As editor of this volume, I see any way that brings the diverse range of disciplines closer together and understanding each other's knowledge as highly productive. However, it is hoped that within the volume there will also be much to help other earth scientists. Every attempt has been made to make the entries as authoritative and up-to-date as possible with latest reference lists and a range of cross-references which will help in the navigation of this volume.

Why the title – *Encyclopedia of Modern Coral Reefs – Structure, Form and Process*? Again, to some extent, it is to make it attractive to multidisciplinary readers. “Cainozoic” or “Quaternary” could have been used but the technical terms may have made it less attractive to other disciplines. Also, modern coral reefs have a continuous lineage with the earliest Palaeozoic reefs, hence the few entries which cover earlier reefs and their influence on today's living reefs in the volume. Structure,

form, and process are the essential ingredients in the earth science recipe for understanding coral reefs as well as most other landforms.

During the last 100 years, coral reefs have attained new values beyond the support of local subsistence economies. They have provided sites for navigational aids and in days of aircraft with limited range, stopover refuelling sites. During World War II many mid-oceanic atolls had strategic importance and following the war, some became testing sites for nuclear weapons. Ironically, the drilling associated with this testing did much to extend the knowledge of the origin of reefs and in particular, support Charles Darwin. Reefs are important sites for commercial as well as subsistence fishing, and further economic value has been added by tourism.

Unfortunately, the future for coral reefs is very uncertain. They are one of the ecosystems most at risk from global climate change and because of this have achieved much prominence in recent times. They have been compared to canaries in coal mines, providing early warning of increasing risks! Both public and scientific perspectives on the impacts of global warming on coral reefs have changed over the last 20 years. Initially a rise in sea level was seen as positive, encouraging new coral growth over largely dead reef flats, although at the other extreme were forecasts of reefs being drowned, all reef islands disappearing and even the reefs themselves being eroded away and tropical coastlines losing their protection. More balanced responses have come as scientists working on processes opened up a range of possibilities. Earth science has played a major role in these revisions especially where cooperation with other disciplines has provided balanced assessments. Impacts will be severe with bleaching from temperature rise and calcification rates declining in response to acidified oceans, leading to unsustainable growth rates of corals and many other important organisms. The earth science focus here is on the impact on sediment budgets and the transportational ability of waves. Many scenarios are possible including an increase in available sediment over the reef top, and, with deeper water greater ability of waves to move both this new sediment and that which may have rested on the reef top for several thousand years, towards any preexisting reef island. At least in the foreseeable future, the actual volume of reef islands may increase, though new areas added will lack vegetation and soils and may be at the expense of the areas which have supported subsistence agriculture for millennia.

What is becoming more apparent, as further research into the impact of climate change on reefs is carried out, is that in many instances there are important thresholds

which determine the severity of response. Climate change impact is undoubtedly the most important focus of coral reef research in all disciplines at present. To some extent, the situation is similar to that of the nineteenth century when conflicting hypotheses on the formation of coral reefs were the highlight. Then, as further research revealed the depth and lithology of the foundations, ideas on glacially controlled sea levels became accepted and the whole new scenario of plate tectonics was revealed, it became clear that as in many areas of science, there may be more than one correct answer to a problem. As more thresholds are determined, different options for coral reefs to move into the future will become apparent. Unfortunately, these will mostly be under adverse conditions.

Climate change and coral reefs form one of the major foci of this encyclopedia. Although entries are presented in alphabetical order, they have been organized under major compilation headings which should become particularly obvious when the reader uses the cross-references with each entry. Theories and hypotheses, from Darwin to climate change, also provide a substantial number of entries, together with some of the major methodologies used in the hypothesis testing. Short biographies are given of some of the major contributors to the study of coral reefs in the earth science field, including organizations. Classifications of various features are given, which again show that there may be more than one critical approach to features or processes. Although the encyclopedia does not contain a formal glossary, there are many short entries explaining specific features or processes. As coral reefs vary around the world, a significant number of entries have been devoted to geographical areas. Finally, the past contribution to modern reefs is not forgotten with contributions on specific reef complexes of the geological past, whilst the future, however fragile, is assessed through a number of contributions on conservation.

This is not an exhaustive list but hopefully, it gives a structure to the encyclopedia's contents. Of equal value are the many references given with the entries. These range from some of the most classical to material only published in the last 12 months. The interest in coral reefs is such that, over the next few years, further interesting material will be published and updates may be required, but the 260 entries within the present volume, written by authors from 15 different countries, give a wide perspective of earth science's interest in an increasingly fragile ecosystem.

David Hopley  
September 2010

## Acknowledgments

A work the size of this encyclopedia inevitably relied on the help and cooperation of a very large number of people, only some of whom can be identified. My particular thanks go to the Editorial Board, an international group of highly respected coral reef scientists. To Guy Cabioch, Peter Davies, Terry Done, Eberhardt Gischler, Ian Macintyre, Rachel Wood, and Colin Woodroffe, thank you for keeping this project on course by helping to choose the topics which form the entries, suggesting high-quality authors, reviewing the initial manuscripts, and finally checking the proofs with your selected groups of authors as well as writing important contributions yourselves.

This leads to the largest group I wish to acknowledge, the authors of the 260 entries which range in size from a few hundred words up to major contributions of 10,000 words. Many authors have also taken on more than one entry within their speciality area. Also, with authors from 15 different countries for many, English is not their first language, yet, with help from the Editorial Board and from Springer, they have provided quality articles. Inevitably, with such a large group of people there have been problems with illness, with members of their family, etc. and yet, the overall production has not deviated to any great extent from the original timetable. The writers of the articles are highly commended for their dedication to the work.

At the production end of this project has been the staff of Springer. Their help, understanding, and cooperation, especially when small problems arose, is something I cannot appreciate enough. Their patient collaboration with authors and board did much to maintain the smooth timetable. Special acknowledgment must go to Petra van Steenbergen, Sylvia Blago, and Simone Giesler, who were involved with the encyclopedia from start to finish, a period of over 3 years. In particular, their decision to accept so many color illustrations has done much to add to the attractiveness and interpretation of these entries on coral reefs. Advice, especially in the formative stages, from Charlie Finkl, himself a coastal scientist, and a Series Editor for the *Encyclopedia of Earth Sciences Series*, did much to guide the project along the most effective tracks.

In many works like this, thanks are expressed to the editor's/author's spouse for their patience and support. My appreciation to Patricia goes far beyond this as without her many hours of support, the project would not have been completed. Not only did she run an efficient office, maintaining a most complex filing system and, due to my own deficiencies, taking on responsibilities for all communications but also she provided continuous motivation through the many hours she spent, furthering the project.

Finally, to the many unnamed people who have contributed to the encyclopedia, thank you for your time and effort and I hope the final product meets with your approval.

# A

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## ACANTHASTER PLANCI

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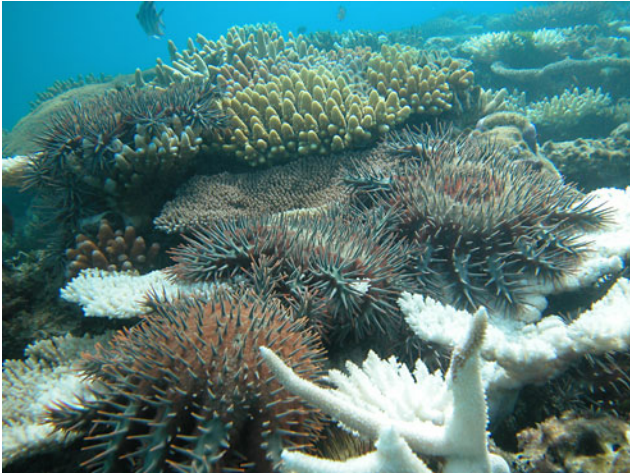
*Acanthaster planci* (Class Asteroidea; Order Spinulosida; “crown-of-thorns sea star or starfish”) is a large (up to 70 cm), mobile, multi-armed (7–23) sea star covered in sharp, toxic spines. It feeds almost exclusively on hard corals and is found on coral reefs throughout the Indo-Pacific. No other reef sea stars remotely resemble its appearance, nor possess comparable life-history traits as a predator on corals.

Crown-of-thorns are prone to population outbreaks, with aggregations of thousands or more adults per hectare not uncommon (Figure 1). Such populations often advance in fronts through coral habitat, leaving formerly luxuriant coral areas dead in their wake. The sea star has a number of life history traits that predisposes these destructive population outbreaks: absence of any equivalent coral predator (little competition for food); a large stomach (that is pushed out through the mouth to digest coral tissue externally); a high fecundity (a mature female can produce some 50 million eggs); planktonic larvae (that can feed in the water column and disperse over long distances); rapid growth ( $\sim 10 \text{ cm.y}^{-1}$ , that is faster than any other coral reef sea star); large size and toxic spiny armature (that provide protection from potential predators); multi-armed morphology and tube feet (allowing them to climb and feed in nearly any position). Repeated population outbreaks have decimated hard corals throughout the Indo-Pacific over the last 50 years.

Outbreaks were first observed in the 1960s. The geographical extent (two oceans) and impact (an ecosystem changed from one dominated by hard corals to one dominated by algae), shocked scientists. A key management issue was whether human activity had somehow precipitated the population outbreaks. Two main hypotheses have been developed that implicate anthropogenic factors. The first is “the predator removal hypothesis” (Endean, 1969), which holds that overfishing (in particular sweetlips (Family Lethrinidae), some wrasses (Family Labridae) and some triggerfish (Family Balistidae)) and collecting of predators of the sea star (notably a large Gastropod mollusc the giant triton *Charonia tritonis*), allow crown-of-thorns to build up in numbers on a reef. On reaching a critical abundance, their reproduction and larval dispersal leads to successful recruitment of larvae on reefs downstream in prevailing currents. A cascade of outbreaks across tracts of neighboring reefs ensues. The second hypothesis (possibly synergistic with the first) is “the nutrient enrichment hypothesis” (Birkeland, 1982, Lucas, 1982). In this scenario, river runoff from human-modified catchments enhances nutrients in coastal waters, resulting in an increase in phytoplankton upon which the sea star larvae feed. Because crown-of-thorns produce such a vast quantity of eggs even a small increase in survivorship leads to larger settlement of larvae onto a reef, which in turn leads to a primary outbreak.

Today, despite repeated outbreaks and years of research the exact events leading to the initiation of an outbreak remain enigmatic. This is because the life-history of crown-of-thorns makes it difficult to disentangle the natural processes leading to an outbreak from those forced by human activities. As a result crown-of-thorns remains a major management problem for coral





**Acanthaster Planci, Figure 1** A crown-of-thorns feeding aggregation. Such outbreaks of the sea star are a major recurrent cause of coral mortality on coral reefs throughout the Indo-Pacific (photo: AIMS LTMP).

reefs. Where adults have been collected as a control measure, coral has been saved from predation only over relatively small areas (hectares). In the past, coral cover has generally recovered within 10–15 years of an outbreak. However coral resilience in the face of future outbreaks is uncertain (Done, 1987). This is because the size and frequency of other impacts that can effect coral reefs (such as cyclones, coral bleaching, and ocean acidification) are predicted to increase in coming years due to greenhouse gas emissions. Without full recovery, repeated outbreaks will eventually lead to the degradation of the coral reef community.

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## Cross-references

[Coral Reef, Definition](#)  
[Corals: Environmental Controls on Growth](#)

## ACCOMMODATION SPACE

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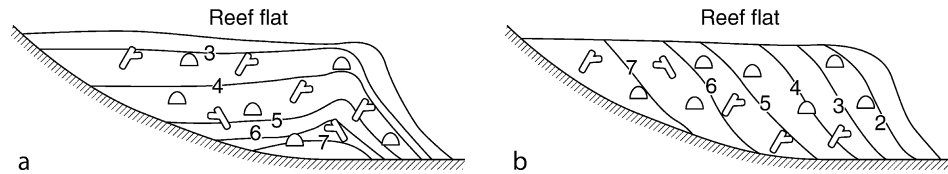
### Definition

The space available, in both a vertical and a lateral sense, within which corals can grow, increase framework and sediments accumulate.

### Accommodation space

For corals, accommodation space is constrained vertically by the water-air interface and its volume broadly determined by reef widths and slope angles. For sedimentary accumulations on reef platforms, the lower boundary is governed by reef margin position, reef flat elevation and lagoon depth and the upper boundary set by the height of wave run-up during storm events. The rate at which accommodation space can be filled depends upon rates of vertical coral growth, vertical framework accretion and sediment supply, transport and accumulation; these are all controlled by reef productivity and sediment generation processes which may themselves be constrained by the environment processes (e.g., wave exposure locally prevents coral growth from filling accommodation spaces on Hawaii; Grigg, 1998), be periodically interrupted by storms (see *Tropical Cyclone/Hurricane*) and modulated by sea level change, which ultimately determines the upper margin of the accommodation space (Figure 1).

Over the long-term, a subsiding reef basement results in an increase in accommodation space. During glacial periods, emergent reefs were subject to subaerial solution, thus increasing the vertical accommodation space available for reef re-growth on renewed inundation during interglacial periods. There has been debate over the subaerial erosion rates involved, and thus the additional accommodation space generated, ranging from minimal downwearing (e.g., Quinn and Matthews, 1990) to 6–63 cm of surface lowering per 1,000 years (e.g., Gray et al., 1992). During the stable sea-level of the late Holocene, there has been “turn-off” of both vertical and horizontal growth of some reefs due to the progressive thinning of accommodation space as reefs approached present sea level (which itself may have fallen slightly in some Indo-Pacific locations, thus further reducing accommodation space) and the difficulty of lateral expansion, and maintenance of reef front volume and integrity, over relatively unstable reef front talus deposits in increasing water depths. For example, Smithers et al. (2006) attributed the shut-down of fringing and nearshore reef progradation on the Great Barrier Reef between 5.5–4.8 ka BP and 3.0–2.5 ka BP to the contraction of accommodation space caused by the reefs’ own growth and the complete occupation of favorable reef foundations. In the short term, local accommodation space is an outcome of local reef erosion and the re-configuration of sedimentary accumulations resulting from hurricane and



**Accommodation Space, Figure 1** Different models of fringing reef development show different modes of accommodation space filling. (a): accommodation space is filled by corals showing catch-up or keep-up behavior. (b): reef accretion is lateral, having established at a level with little or no vertical accommodation space. Isochrons are in thousands of radiocarbon years BP (From Kennedy and Woodroffe, 2002).

cyclone impacts (see *Tropical Cyclone/Hurricane*). It has been argued that rates of sea level rise of  $\sim 0.5$  m by AD 2100 might create new accommodation space and switch reef vertical accretion back on, with carbonate production for the entire Great Barrier Reef rising from the current estimated  $50 \text{ Mt a}^{-1}$  to  $70 \text{ Mt a}^{-1}$  (Kinsey and Hopley, 1991).

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### ACROPORA

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### Synonyms

Arborescent corals; Axial branching corals; Midori ishi (Japan); Staghorn corals; Table corals

### Definition

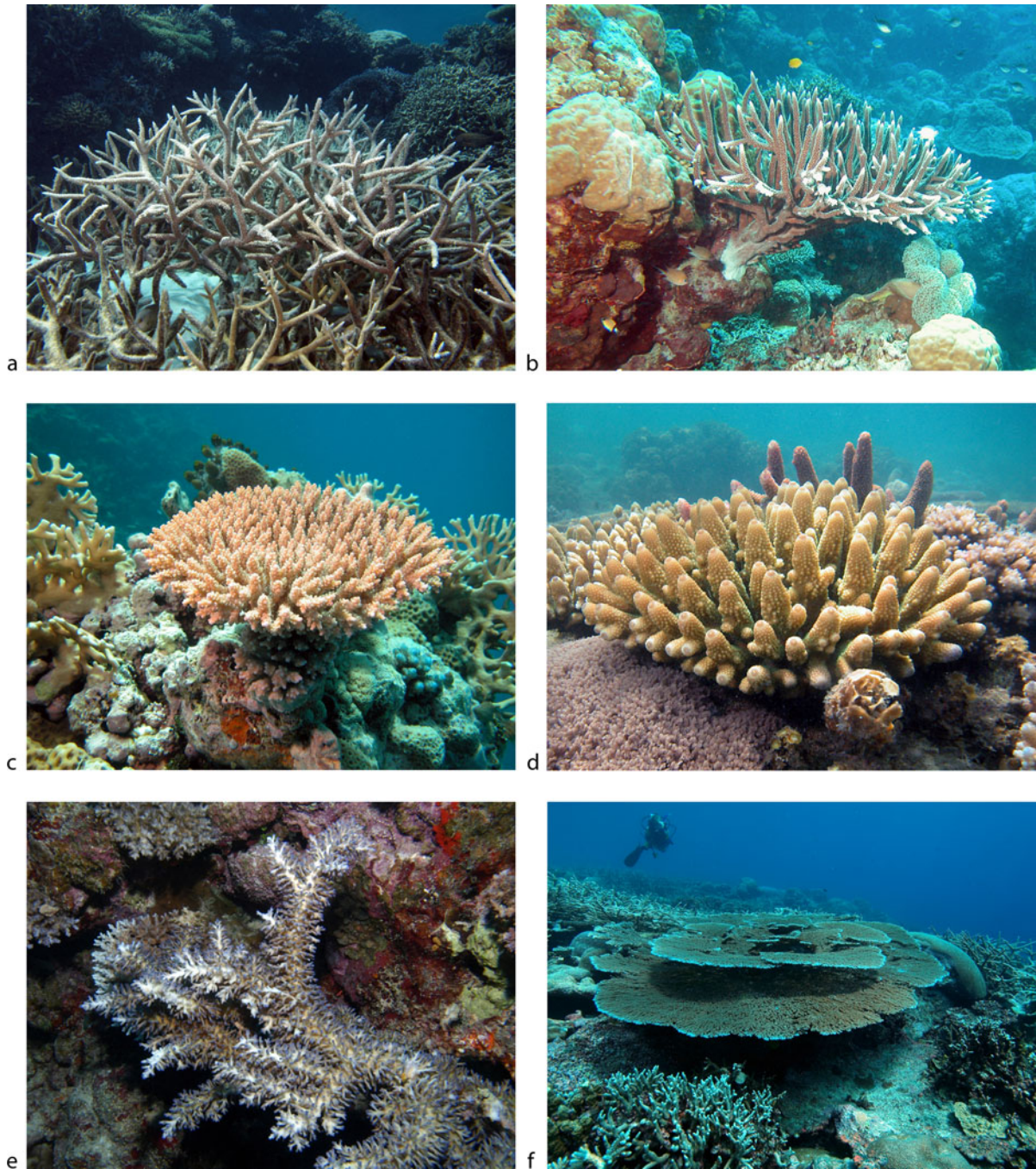
*Acropora* (Oken, 1815) is the type genus of the hard coral family Acroporidae (class Anthozoa, order Scleractinia

of the phylum Cnidaria). Currently, around 120–140 living species are recognized in this genus, but new species are still being discovered in both living and fossil coral assemblages. The Latin name derives from the growth mode, where branches are formed by a central or axial polyp, which buds off numbers of a second kind, the radial polyps, from around its tip as it extends. New branches are formed by the development of new axial polyps along the branch. This mode of growth, which is similar to the axial mode in flowing plants, allows many variations on a branching theme (Figure 1). It is thought to have been a key character in the evolution of a diverse array of species in *Acropora*, although other processes are also proposed, such as hybridization and reticulate evolution facilitated by the mass spawning of related species.

### Introduction

Six coral families (Acroporidae, Faviidae, Mussidae, Poritidae, Fungiidae, and Pocilloporidae) dominate modern world reef composition, in terms of diversity, abundance, geographic range, and contribution to accretion of reef carbonates. Of these, Acroporidae is arguably the most successful, as the two most species-rich genera, *Acropora* and *Montipora*, allow it to dominate the species diversity and coral cover of most Indo-Pacific reef locations. *Acropora* the “staghorn” corals have played a role in the biodiversity, ecology, and structure of coral reefs for almost 60 million years (Schuster, 2003; Wallace and Rosen, 2006). Their mode of skeletal construction, where polyps are supported within an open “synapticular” framework (Figure 2), allow for rapid growth with efficient use of calcium carbonate (Gladfelter, 2008) and provide habitat complexity for other reef biota (Munday, 2002). Strong representation in mass coral spawning and recruitment events, and rapid recolonization after destructive natural events are the characteristics of *Acropora* (e.g., Babcock et al., 1986; Connell et al., 2004): however, this genus may experience severe localized or widespread loss of diversity from major perturbations such as coral bleaching due to elevated seawater temperature, cold-water events, tsunamis, cyclone damage, and predator population outbreaks, particularly of *Acanthaster planci*, the crown-of-thorns sea star (Wilkinson, 1998–2008; Berklemans et al., 2004; Marshall and Baird, 2006). Chronic anthropogenic impacts such as nutrient and sediment run-off,





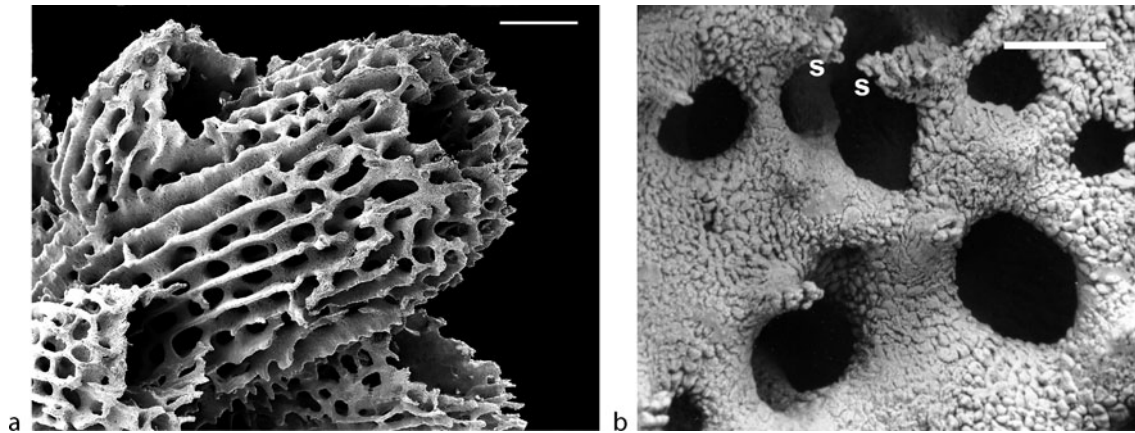
**Acropora, Figure 1** Examples of colony shapes in *Acropora*: (a) Arborescent (*A. grandis*), (b) Arborescent table (*A. valenciennesi*), (c) Corymbose (*A. anthocercis*), (d) Digitate (*A. gemmifera*), (e) Hispidose (*A. echinata*), and (f) Table (*A. clathrata*). (Photos: P. Muir.)

overfishing, and coral mining for limestone also have an impact on *Acropora* (Fabricius, 2005; Fabricius and Wolanski, 2000; Brown, 1997).

### Nomenclatural issues

Until the late nineteenth century *Acropora* was known mostly as *Madrepora*, a broadly applied name, which is

now restricted to a genus of non-zooxanthellate deepwater corals. The name *Acropora* was stabilized by a decision of the International Code of Nomenclature in the mid-twentieth century (Boschma, 1961; China, 1983), which also ruled on a type species, *A. muricata* (Linnaeus, 1758). A dilemma concerning the nature and provenance of this species, described by Linnaeus as being from the



**Acropora, Figure 2** (a) Synapticular formation of *Acropora* skeleton, shown in scanning electron micrograph of *A. abrotanoides*. Also seen is the axial corallite (a) and radial corallites (r) (Scale: 500  $\mu$ m). (b) High power SEM of synapticular formation in *Acropora nasuta*. Two synapticalae approaching each other will form a node (n), from which another synapticala will develop at right angles (Scale: 100  $\mu$ m). (Photos: P. Muir and C. Wallace.)

“Asian Sea,” was resolved by designation of a neotype from central Indonesia (Wallace, 1999). The size of the genus was reduced slightly by elevation of a subgenus *Isopora* to separate genus status because it differed from other *Acropora* in skeletal and reproductive morphology as well as reproductive mode (Wallace et al., 2007). The remaining species are organized into 20 species groups based on skeletal features (Veron and Wallace, 1984; Wallace, 1999). Genetic studies are revealing numerous dilemmas about species boundaries (Van Oppen et al., 2001, 2002) and at least one named species of *Acropora* is now known to be an F1 hybrid (Van Oppen et al., 2000; Vollmer and Palumbi, 2002).

### The skeleton and polyps

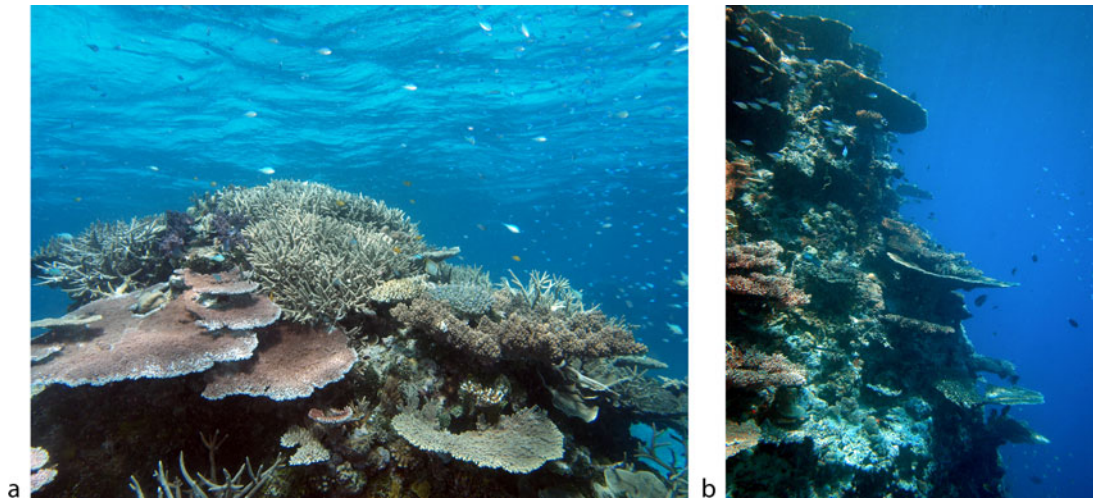
All scleractinian corals have skeletons of the crystal aragonite form of calcium carbonate, but formation of a skeleton by the polyps follows different patterns among families, giving structural features by which corals can be identified in both living and fossil form (Wells, 1956; Roniewicz, 1996). In Acroporidae, most components of the skeleton are formed by the development of simple rods or “synapticalae,” which allow for a strong but light and open growth (Figure 2; Nothdurft and Webb, 2007; Rosen, 1986). The potential of this mode for rapid growth in three dimensions is exemplified by the axial growth of *Acropora*. This provides a light scaffolding to support the living colony and allows organization of the tissues into a gastrovascular system in which flagellated gastrodermal cells promote laminar flow up, down and around the branch to transport water and nutrients. The axial polyp extends through most of the branch and is thus much longer than the radials. A notable aspect of the growth mode of *Acropora* is that some species have symmetrical growth around a central growing point and maintain a limited “determinate” pattern of growth, while others exhibit unlimited and asymmetrical growth, filling

in available space wherever it comes up. These contrasting modes allow *Acropora* colonies to efficiently fill available space on the reef (see Figure 3a). The polyp cavities are extended by the coenenchyme, a complex network of tubules containing extensions of the gastric cavity. Much of the skeletal variation used for taxonomic delineation of species comes from the shape of the radial corallites and the microstructure of the skeleton (Wallace, 1999). Another form of skeleton, the epitheca, formed by calcite form of calcium carbonate, is present in very small quantities below the living tissues of the branch and acts as a sealant preventing infection and protecting the live polyps and coenenchyme from fluid loss (Barnes, 1972). The polyps of *Acropora* have a simple tubular structure and 12 tentacles, one of which extends greatly as a “catch tentacle,” particularly when the polyps are feeding at night (Wallace, 1999). Below the tentacles are the mesenteries, which carry the gonads when they develop and have a muscular internal filament, which can extend outside the polyp for defense, clearing space, and possibly feeding (Roff et al., 2009).

### Habitats and ecology

*Acropora* is often interpreted as being a reef-front genus, favoring sites with good circulation, high oxygen content due to the strong movement of water, and access to food from oceanic waters. While a diverse “*Acropora* zone” from the reef top to about 12 m depth, is indeed a characteristic of most oceanic Indo-Pacific reefs, this genus also occurs significantly in specialized habitats such as sandy lagoon floors, deep reef slopes and deepwater *Halimeda* banks, and in relatively turbid fringing reef locations. The persistence of an abundance of colonies and diversity of species through time on any reef habitat relies on a complex interaction of water quality and physical and biological parameters: the activities of other reef organisms also impact on survivorship at each life stage



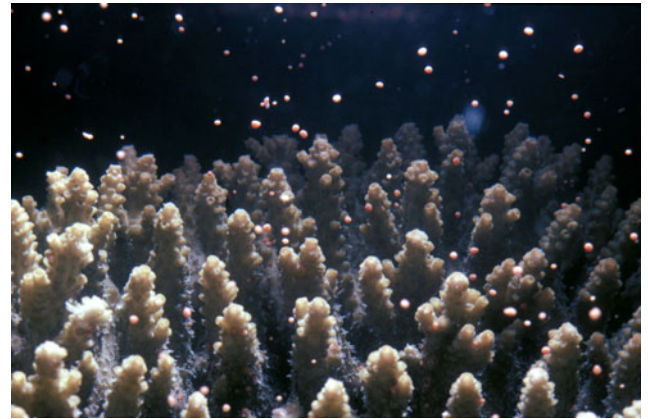


**Acropora, Figure 3** (a) Numerous forms of *Acropora* maximize usage of three-dimensional space in shallow reef shoals: ten species occupy this frame. (b) Steep walls support mainly small plates which maximize exposure of the polyps to light. (Photos: P. Muir.)

and compete with corals for resources (Done, 1999; Done et al., 2007). Human-influenced deterioration of conditions suitable for survival and/or settlement of *Acropora*, or favoring survival and population increase of other benthic organisms such as the coral genus *Porites*, soft corals, and algae, are thought to be involved in the gradual deterioration of *Acropora* communities in many parts of the world and to threaten the survival of the rarer or more narrowly distributed species of this genus (McClanahan et al., 2008). Many rare species may be threatened by diminishing habitats (Carpenter et al. 2008), although it has been suggested that some rare species with small global population sizes are actually unidirectional hybrids, and that this contributes to increased genetic variability and adaptive potential, making them less vulnerable to extinction (Richards et al., 2008). In the Caribbean, the two major *Acropora* species *A. cervicornis* and *A. palmata* have undergone massive population loss over recent decades in many locations as a result of exposure to repetitive hurricanes, coral diseases, changes in water quality, and outbreaks of other reef organisms (Bythell et al., 1993; Williams et al., 1999) and such rapid declines appear to be unprecedented in the past 4,000 years (Aronson and Precht, 1997).

### Sexual and asexual reproduction

Species of *Acropora* reproduce sexually by developing gametes (eggs and sperm) along the mesenteries (radial dividing structures) within the polyps. In *Acropora* polyps have both sexes (hermaphrodite), with certain mesenteries bearing eggs and others sperm (Wallace, 1985) (Figure 4). Fertilization takes place externally, after the gametes are released into the water column, often during mass spawning events involving many species. The fertilized eggs develop into ciliated larvae known as planulae,



**Acropora, Figure 4** Egg sperm bundles of *Acropora tenuis* leaving polyps and ascending into the water column, during a mass spawning event on the Great Barrier Reef, Australia. (Photo: Z. Florian.)

which spend some days in the water before being ready to settle on reef surface to begin a new colony. Planulae remain viable for days to weeks and may be transported long distances and settle away from the home reef. This contrasts with sexual reproduction in the sister genus *Isopora*, where sperm is released but the eggs stay within the polyp, where they are fertilized by sperm from other colonies and develop into larvae which are released ready to settle on the reef. The two contrasting modes of reproduction may have different consequences for the genera after loss of the adult corals in a population: for *Acropora*, the possibility of recruitment of larvae from healthy reefs is greater. This has been seen after mass bleaching of *Acropora*, for example, in the Maldives (Wallace and Zahir, 2007) and Socotra (western Yemen), where

*Acropora* recruits were visible several years before the appearance of *Isopora*, following the 1998 bleaching event (L. DeVantier, personal communications).

### Genetics and phylogeny

*Acropora* has a large and complex genome and this has been studied in detail for certain species and species groups as well as in the context of genus-level phylogenies. Molecular (genetic) studies show corals to have two main evolutionary lines, known currently as the “Robust” and “Complex” clades. *Acropora* and other members of the family Acroporidae fall within the Complex clade (Romano and Cairns, 2000; le Goff-Vitry et al., 2004; Chen et al., 2002). Evolution of the mitochondrial genome of all Anthozoa is typically slower than that of other animals, making it difficult, for example, to use cytochrome b to study population genetics in these animals, but it is faster in *Acropora* than in confamilial genera (Van Oppen et al., 1999). The tempo of evolutionary change is faster in the nuclear and slower in the mitochondrial genomes for *Acropora* (and other corals studied), making them more similar to plants than other animal groups in this respect (Hellberg, 2006; Chen et al., 2009). Genetic studies and laboratory cross-fertilization experiments on *Acropora* from within species groups (especially the *A. aspera*, *A. cervicornis*, and *A. humilis* groups) have indicated that hybridization and introgression may play a significant role in maintaining variety within populations and associations of *Acropora* species, perhaps contributing to resilience in the face of adverse conditions (Van Oppen et al., 2000; Wolstenholme et al., 2003). These and many other genetic findings for *Acropora* and other corals are contributing to a major revision of the characteristics and relationships within the order Scleractinia. Because corals have a hard skeleton and this remains after death, there is a superb fossil record and long-known paleontological information is currently being integrated with the molecular results to develop a new overview of relationships and evolution.

### Biogeography and evolution

The greatest living diversity of *Acropora* is seen in Indonesia, where 91 species have been recorded (Wallace, 2001) and similar numbers are present in the Philippines and Papua New Guinea. The Indonesian diversity is greatest within the region known as “Wallacea,” that is, the region of islands between the Asian and Australian continental shelves (Wallace, 2001). The Indonesian *Acropora* diversity includes species with very extensive Indo-Pacific ranges, others restricted to the central Indo-Pacific, and yet others which have either predominantly Pacific Ocean or Indian Ocean distribution, with some overlaps in Indonesia. (Wallace, 2001; Wallace et al., 2001). In the Caribbean, only three living species occur. Through post-Cretaceous time, *Acropora* has been present in all the major reef-bearing parts of the world, including

the fossil deposits of the Middle East and Europe, fossil and modern reefs of the Caribbean and the Indo-Pacific, where the majority of the living species occur. It is known in the fossil record from the Paleocene of Somalia (approx. 60 million years ago) and was possibly present before the end of the Cretaceous (Baron-Szarbo, 2006). Nine of the twenty species groups are represented in the mid-Eocene fossil record of England and France and this is taken to indicate that the diversification of this genus began well ahead of its later Indo-Pacific diversification (Wallace, 2008). Several species of *Acropora* also await description from the Oligocene to early Miocene of Europe and Miocene-Pliocene of the Caribbean. The first case of *Acropora* being abundant and dominant on a coral reef is seen in the Oligocene of Greece (Schuster, 2003).

### Summary

*Acropora*, the staghorn coral genus, has persisted for some 60 million years and now remains in living form in the Caribbean and the Indo-Pacific, the two main reef-bearing regions of the world. It is regarded as extremely successful because it contains the greatest number of species of any coral genus, and its species typically occur in great abundance. While it plays a major role in many aspects of reef ecology, *Acropora* has been shown to be extremely vulnerable to major disturbances on reefs, and thus there is concern about its persistence into the future, in the face of changes due to bleaching, disease, and other factors resulting from global climate change. The fossil record tells us that this genus has persisted and diversified through time, and genetic research is indicating that rare species may have a resilience to local extinction because of the potential for hybridization with other species. Recent decadal changes in both the Caribbean and the Pacific, however, show that *Acropora* can undergo local extinction in certain circumstances. It is clear that the future of this coral genus is intimately linked with the future of the world’s coral reefs.

### Acknowledgments

Dr. P.R. Muir of Museum of Tropical Queensland for preparing figures and reviewing text.

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## Cross-references

[Carbonate Budgets and Reef Framework Accumulation](#)  
[Corals: Biology, Skeletal Deposition, and Reef-Building](#)  
[General Evolution of Carbonate Reefs](#)  
[Porites](#)  
[Scleractinia, Evolution and Taxonomy](#)

## ADAPTATION

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### Definition

*Adaptation* is the process of change in the structure or function of an organism or parts of an organism that makes it better suited to the environment in which it lives. Adaptations (or traits that are adaptive) that are heritable, i.e., coded in genes or that have consequences on the reproductive success of genes, contribute to natural selection.

*Acclimatization* refers to adjustment to local conditions that occurs within the lifetime of an individual, in response to external environmental conditions, for example, through behavioral changes, or increased tolerance of stressful conditions. *Acclimation* is similar, though is applied more narrowly to artificial conditions and experimentation. Both can lead to true adaptation if and when the relevant traits are passed on to the next generations.

### Introduction

Adaptation is a core concept of evolutionary biology, its significance recognized by Charles Darwin (*Darwin, Charles (1809–1882)*) as a central tenet of his theory of evolution by natural selection (Darwin, 1856). Simply stated, differences in individuals of a species, or among species, may confer differential survival or performance, and thus influence which individuals survive and

reproduce, and thereby the passing of favorable traits on to offspring. Where traits shift or adjust to suit local conditions, beneficial ones can be viewed as “adaptations,” and may confer evolutionary success.

Adaptation is a whole-organism phenomenon. Change in a trait that confers benefits in one area but imposes costs or dysfunction in another may not lead to adaptation if the costs outweigh the benefits. Thus tradeoffs between traits are an essential part of the process of adaptation, placing constraints on what changes are beneficial. This is recognized in life history theory, which relates how organisms divide limited energy and resources to different functions and processes, how the balance between these may change with external conditions, and how these changes result in differential success among life history strategies (Stearns, 1992).

Adaptation is such a wide-ranging process that generalizations about it are often not true in all conditions. For example, severe environmental conditions may pose strong selective pressures leading to rapid adaptation to environmental stress in that part of the population that survives (Hoffman and Parsons, 1991). In this case, adaptation occurs by extermination of “unfit” genes under rapid environmental change. On the other hand, benign conditions enable beneficial traits to accumulate in a population over successive generations. In this case, adaptation occurs by competitive success of beneficial genes over less-fit genes. Not all traits that occur in an organism are certain to be adaptive; they may simply not have a negative impact on the individual’s or species’ survival. Thus, it is necessary to determine specifically if a trait is adaptive through careful observation or experimentation, rather than by simply observing its presence (Gould and Lewontin, 1994). The evolution and taxonomy (*Coral Cay Classification and Evolution*) of extant reef corals provides key insights into the unusual evolutionary pressures faced by corals and hence of their capacity for adaptation.

Coral reefs are typically considered to occur in relatively benign and stable environmental conditions (*Corals: Environmental Controls on Growth*), with high density and diversity of organisms. This creates conditions for high levels of niche diversification and diversification of interactions, and for these to become stable over time. Thus adaptation, or coadaptation (among mutually interacting species), is common on reefs and can be distinguished in many forms of interactions, such as:

1. Primary production: Different functional groups of primary producers, characterized by whether they form hard crusts that resist herbivory and cement reefs, fast-growing low-biomass algal filaments and turfs with high recovery rates from removal, and large-bodied fleshy algal fronds that resist herbivory through low palatability and compete with other sessile organisms to monopolize space (*Algae, Coralline; Algae-Macro; Algae, Turf*);
2. Predator–prey dynamics: A vast array of different prey and predators, and of defense and predation mechanisms. Adaptations of fish consumers are clear in their jaw structures toward their prey (*Figure 1*): scraping



herbivores with hard fused teeth that can graze algal crusts, fish with long tubular mouths for sucking polyp tissue out of a coral skeleton, or top predators with needle-sharp pointed teeth for grabbing fast swimming prey and holding it until it can be torn and swallowed. Defense mechanisms may be even more numerous including chemical defenses of unpalatable algae and invertebrates that produce toxins, hard-shelled defenses such as in snails and crustaceans, or mimicry by palatable species of unpalatable or poisonous species often in completely different taxonomic groups;

3. Mutualisms: With limited space on a coral reef, numerous organisms adapt to live together cooperatively, in stark contrast to predator–prey or competitive interactions, in which one wins over the other. Many species live in or on one another, such as many types of crustaceans and anemones living on anemones and hard and soft corals, or fish and shrimp that share skills to build, maintain, and defend a burrow, or of microscopic single-celled algae such as zooxanthellae living in the tissue of a host such as a coral, to the mutual benefit of both.

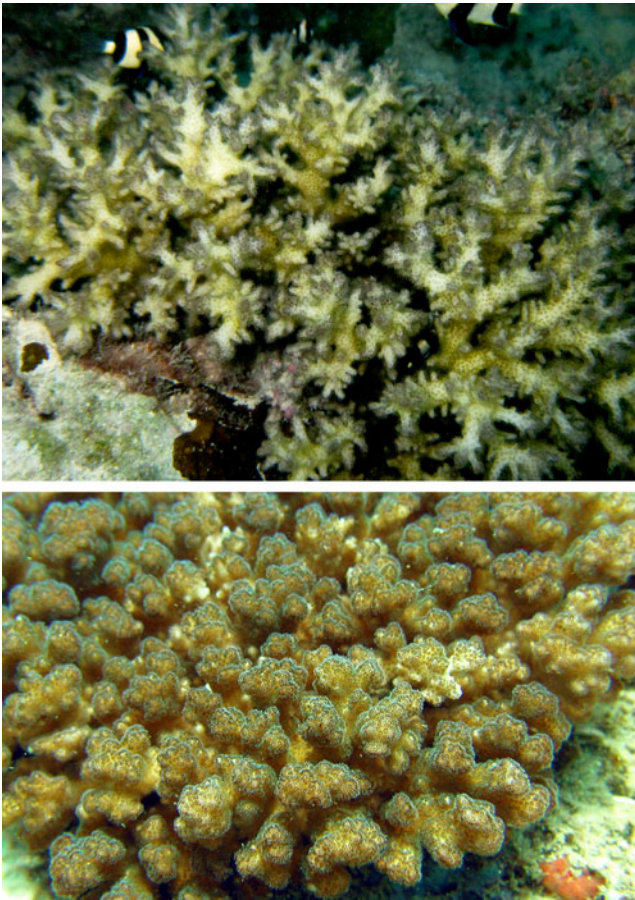
### Coral–zooxanthellae symbiosis as an illustration of adaptation

The symbiosis between corals (the host, a sessile macroinvertebrate) and its zooxanthellae (the endosymbiont, an autotrophic single-celled algae) is the example *par excellence* of a type of partnership that has recurred among different partners in shallow tropical seas for hundreds of millions of years. The host is attached (sessile) on a shallow bottom, providing a sheltered nutrient-rich microhabitat in the photic zone for the endosymbiont. The endosymbiont fixes energy of sunlight into carbohydrates, which are passed to the host for consumption, and may also enhance the intracellular chemical environment for cellular processes of the host, such as calcification (*Corals: Biology, Skeletal Deposition, and Reef-Building*). The adaptations enabled by this symbiosis can be illustrated at physiological, organismal, and ecological–geological scales.

Because the symbiosis combines two organisms – a photosynthetic algae and a consumer animal – two forms of energy capture and nutrition are possible. Under low-nutrient, high light conditions, photosynthesis is maximized, tight nutrient-cycling between the symbiotic partners enables growth in both, and autotrophy is the dominant mode of energy capture for the holobiont. By contrast, in highly turbid environments with limited light, heterotrophy by the coral predominates. Under these conditions feeding by the coral on plankton, detritus, and dissolved organic matter (*Corals: Environmental Controls on Growth*) may compensate for limited autotrophy and enable corals to thrive. The reliance of different coral species on autotrophy vs. heterotrophy, and their ability to shift



**Adaptation, Figure 1** *Top* – butterflyfish (Chaetodontidae) have long tubular mouths for sucking polyp tissue out of a coral skeleton, and a flattened shape for maneuvering in narrow spaces between coral branches. *Middle* – hawfish (Cirrhitidae) live on and within coral colonies. *Bottom* – parrotfish (Scaridae) have hard fused teeth that can graze algal crusts and excavate the rock substrate.



**Adaptation, Figure 2** Growth form adaptations of *Pocillopora damicornis*, which forms thin delicate branches in calm and deeper conditions (top) and thick robust branches in shallow rough conditions (bottom).

between the two, differs, reflecting adaptations to different environments and ecological niches.

At the organismal level, a classic example of the adaptability of corals is in the diverse growth forms possible in some species. For example, growth form may vary depending on hydrodynamics (affecting how robust the skeleton must be) or light and sediment regimes (affecting shape, orientation, and self-shading (*Corals: Environmental Controls on Growth*). *Pocillopora damicornis* is a fast-growing, opportunistic, branching coral species that illustrates this well (Figure 2): individuals growing in calm and light-limited conditions may have very fine branches (no selection for robust growth but strong selection to minimize self-shading) while individuals of the same species in rough, well-illuminated environments may have very robust branches (resistant to breakage, no need to minimize shading effects). Individual colonies from the extremes of these distributions may appear so different that

without intermediate growth forms being known, these may appear to be separate species (Veron, 2000). Further adaptations of growth form can relate to, for example, sediment shedding in high-sediment conditions.

The ability of coral holobionts to calcify extremely efficiently and thereby produce durable skeletons has enabled successive generations to colonize the skeletons left by previous generations and thereby raise up above the substrate resulting in reef construction over time (*Coral Reef, Definition*). The specific growth forms and other adaptations of the dominant corals in these communities affect the morphology and development of *Reef Structure*. Over geological history different but functionally equivalent symbioses have recurred: rugose corals in the Palaeozoic; rudist bivalves in the Cretaceous; scleractinian corals in the Cenozoic. The fossil reefs they have left behind show characteristic adaptations to the periods in which they lived.

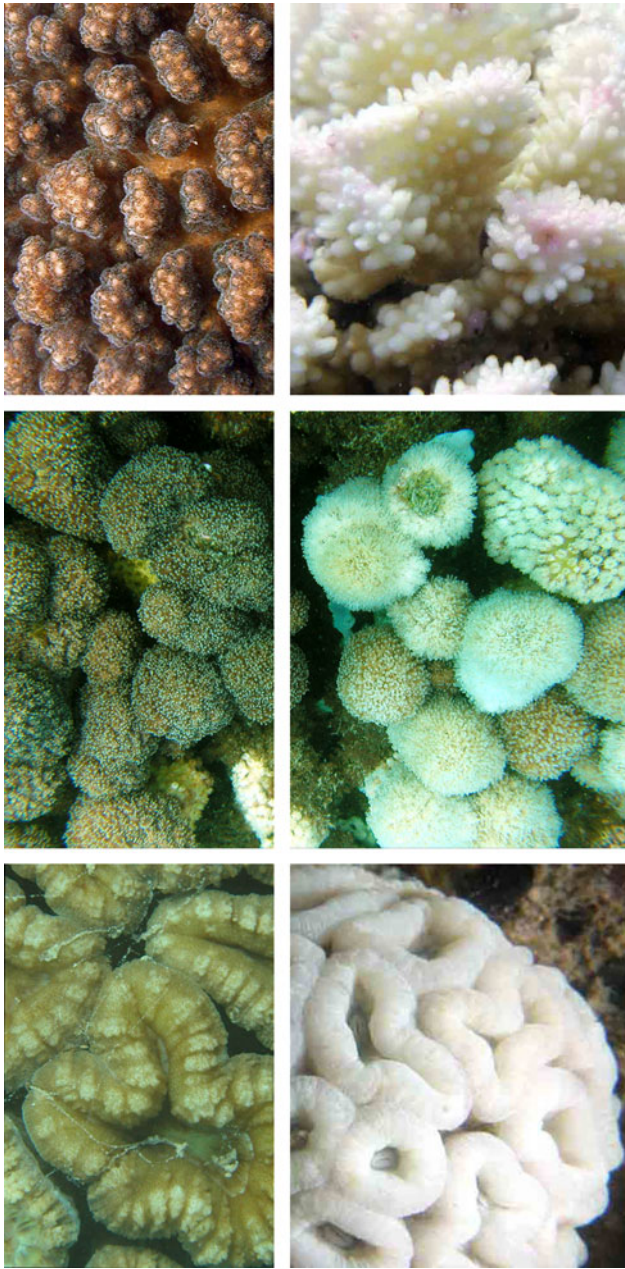
### Current investigations, controversies, and gaps in current knowledge

#### Coral bleaching

The life history of symbiotic corals and the as-yet incompletely understood phenomenon of coral bleaching (*Temperature Change: Bleaching*) provide an interesting case study of adaptation in action. As currently understood, the coral host provides a safe habitat and nutrients to the endosymbiotic algae. They in turn contribute to a range of the coral host's physiological processes by transferring energy from sunlight in the form of fixed carbon, and chemically facilitating a variety of intracellular processes, such as calcification (Muscatine, 1990). The symbiosis is obligate because coral species that are symbiotic do not successfully compete in nature when asymbiotic. However, the symbiosis can be disrupted temporarily as happens under stress (e.g., heat, cold, hyposalinity) when the symbionts part company and the coral “bleaches,” or turns white (Figure 3). This occurs by a reduction in the photosynthetic capacity of the holobiont (by reduction in chlorophyll concentration in individual symbionts, and/or by reduction in symbiont densities), primarily to counter the damaging effects of overproduction of free oxygen radicals by the symbionts.

As a stress response, bleaching must have some capacity for acclimatization and adaptation (Coles and Brown, 2003; Obura, 2009). The Adaptive Bleaching Hypothesis first expressed this idea as a mechanism that allows coral symbionts to adapt to changing environmental conditions (Buddemeier and Fautin, 1993), a position countered by other on the grounds of insufficient evidence (Hoegh-Guldberg, 2005). Further advances in the field may come through seeing bleaching as an extreme state of a range of symbiotic responses to changing environmental conditions (Obura, 2009). These include, from least to most severe: fluctuating symbiont densities, such as occur under





**Adaptation, Figure 3** Bleaching of corals has been portrayed as an adaptation for the coral–zooxanthellae symbiosis to resist stressful conditions, whereby zooxanthellae and/or chlorophyll is lost such that the normal color of the coral (*left panel*) fades such that the white skeleton becomes visible through the transparent coral tissue (*right panel*). All hard coral genera may bleach; shown here are the genera *Pocillopora* (*top*), *Galaxea* (*middle*), and *Lobophyllia* (*bottom*).

normal seasonal changes in the environment; shuffling between different clades of symbionts already in the coral, in response to more extreme environmental fluctuations; taking on new symbiont clades from the water column, after bleaching caused by severe stress. In the latter case,

the switch to different symbionts may be a temporary response to severe stress, with reversion to normal symbiont populations following a return to normal conditions.

There are tradeoffs between high growth and reproduction versus slow growth and stress resistance that affect the bleaching response of corals, illustrating the adaptive dimensions of bleaching. Corals characterized by rapid growth and reproduction and thin coral tissues tend to bleach and die at lower levels of stress (e.g., *Acropora*, *Pocillopora*), while those characterized by slow growth and thick coral tissues tend to bleach and survive at higher levels of environmental stress (e.g., *Porites*) (Loya et al., 2001). Greater tissue thickness and larger polyp size may be adaptive through their shading of zooxanthellae, ameliorating stress from high light and temperatures.

### Long-term change

Global climate change (*Climate Change and Coral Reefs*) is proceeding in multiple environmental parameters critical to coral growth and survival. Water temperature and acidification of ocean waters are two of the fundamental ones (Hoegh-Guldberg et al., 2008), in addition to many others such as changes in sea level, storm tracks, wave regimes, precipitation, and terrestrial runoff that will affect reef growth. The ability of corals and zooxanthellae to adapt to the changes in these basic environmental parameters will fundamentally affect their ability to continue to grow and build reef structures.

Increases in the frequency and severity of coral bleaching events globally are an indicator of water temperatures exceeding the temperature envelopes to which corals are historically adapted. The adaptive potential of bleaching and other regulatory processes is currently unknown (Hughes et al., 2003), however the adaptive basis for coral bleaching explained above, and scenarios for the degree of adaptation needed for corals to survive future change (Donner, 2009), provide tools for understanding this process as it unfolds. The adaptive potential of corals to seawater acidification is less known than that for temperature, and as a basic chemical parameter controlling calcification it may be that there is very little ability for corals and other calcifying marine organisms to adapt to more acidic conditions (*Ocean Acidification, Effects on Calcification*). In this time of global change, the adaptive capacity of corals will be a critical feature in determining how reef ecosystems respond to change.

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## Cross-references

Algae, Coralline  
 Algae-Macro  
 Algae, Turf  
 Climate Change and Coral Reefs  
 Coral Reef, Definition  
 Corals: Biology, Skeletal Deposition, and Reef-Building  
 Corals: Environmental Controls on Growth  
 Darwin, Charles (1809–1882)  
 Ocean Acidification, Effects on Calcification  
 Porites  
 Reef Structure  
 Temperature Change: Bleaching

## AERIAL PHOTOGRAPHY OF CORAL REEFS

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### Aerial photography of coral reefs

Because of the complexity of coral reefs and difficulties in ground survey, the reef environment was one of the

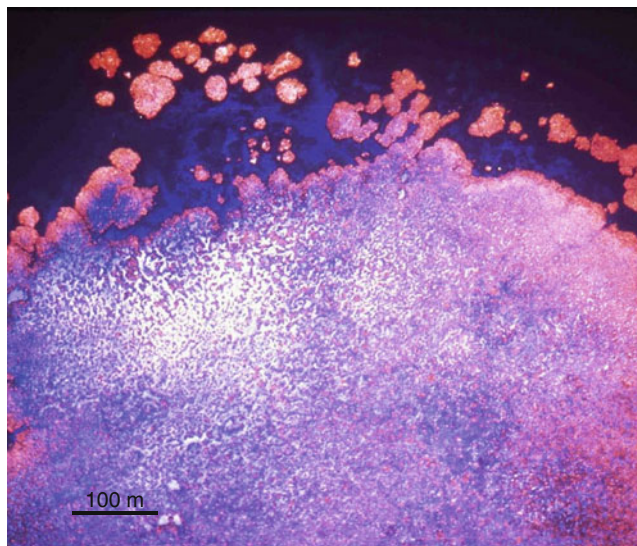
earliest to take advantage of remote sensing techniques (Hopley, 1978). Both aircraft and balloons (e.g., Rützler, 1978) formed the initial platforms, usually for vertically mounted cameras using black and white film. On the Great Barrier Reef (GBR), the earliest vertical aerial photography was in 1925, when the Royal Australian Air Force photographed the Low Isles at a scale of 1:2,400 in 1928 for the Yonge Expedition (see [Great Barrier Reef Committee](#)). Simultaneously, Umbgrove (1928, 1929) was photographing reefs in Indonesia to aid the extensive work he was carrying out there.

Aerial photography was used in many reef studies for the next 50 years, though systematic approaches were rare (Steers, 1945; Teichert and Fairbridge, 1948, 1950). Color photography was used in some areas, especially those related to tourism projects. Between 1964 and 1972, the whole of the GBR was photographed at scales between 1:50,000 and 1:80,000 (later to be used in combination with satellite imagery in providing the detail for the first zoning maps of the GBR Marine Park, Hopley et al., 1989). In the 1970s, experiments were made with emulsions outside the visible range. For example, it was found that the near infrared part of the spectrum (0.7–0.86  $\mu\text{m}$ ), though giving poor water penetration, uses its whole tonal range over only a meter or so of water depth, i.e., was ideal for mapping exposed reef flats at low tide. Moreover, the zooxanthellae within the coral tissue, like terrestrial vegetation, provides a very strong reflective signal (Hopley and van Steveninck, 1977) (Figure 1). Initial experiments were made using both color and near infrared film from flying heights as low as 1,000 ft (Linfoot and Thamrongnawasawat, 1993; Thamrongnawasawat and Catt, 1994; Thamrongnawasawat and Hopley, 1995), providing pixels of <25 cm (Figure 2). As detailed in the quoted references above, the optimal flying height for the Hasselblad Single Lens Reflex 500 EL/M camera used was found to be about 3,000 ft (914 m). A digital image processing system called BRIAN or microBRIAN (Jupp et al., 1985) was used to analyze the scanned data.



**Aerial Photography of Coral Reefs, Figure 1** Branch of living *Acropora* sp. just removed from water and displaying strong near infrared reflectance from the symbiotic zooxanthellae.



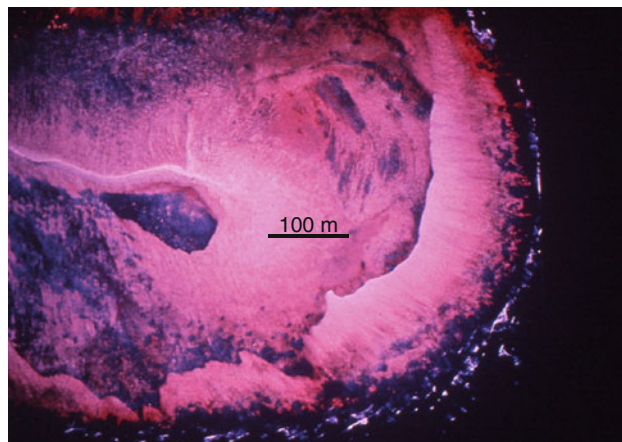


**Aerial Photography of Coral Reefs, Figure 2** Color near the infrared photograph from ~5,000' (1,524 m) of Wheeler Reef near Townsville on the Great Barrier Reef. Tide was a Spring low and features on the reef margin with healthy coral cover show a stronger reflectance than those on the main reef flat, where ca. 0.25 m water cover reduces the IR penetration.

Image combination techniques were applied to merge each pair of true color and infrared digitized photographs into one imagery file (Kuchler, 1984).

While, the near infrared image can penetrate only 1 m of water, the detail of reef flat morphology noted above is very apparent (Figure 3) and it complements the 15–20-m-depth penetration of the color image. Advantages are high resolution, choice of timing (though weather dependent), and modest cost. In an initial experiment mapping Marine Park coral reefs in Thailand for management purposes, it was possible to differentiate between reef flat head and branching corals, seagrass beds and nonliving substrate, with an accuracy between 86.7% and 100% (Thamrongnawasawat and Hopley, 1995). Mumby and Green (2000) provide a critique of the digitized aerial photographic methodology, concluding that it is ideally suited to small area survey.

However, as the resolution and spectral cover of satellite imagery has progressed, it too has the ability to provide ecological data appropriate to management requirements (Mumby and Green, 2000). For the differentiation of ecological zones across reef tops, the latest digital airborne scanners, e.g., the Compact Airborne Spectrographic Imager (CASI), benefitting from the low-level aircraft platforms of aerial photography and the sophisticated scanning technology of satellites, are now arguably the most effective (Mumby and Green, 2000). Its spectral resolution is at least equal to that of satellite imagery. Spatial resolution is also high though dependent on flying height (e.g., from 840 m it is 1 m). Depth penetration can be >18 m. In a comparison of techniques for mapping reefal habitats, Mumby and Green (2000) quote



**Aerial Photography of Coral Reefs, Figure 3** Color near the infrared photograph of Pandora Reef near Townsville, GBR on a medium low tide. The full tonal range of the IR reflectance is used on the features, which are exposed or have a water cover of ~1 m including living coral margins, shingle ridges, and reef flat pools with depths up to 1 m.

81% accuracy for CASI compared with the levels of 57% for 1:10,000 color aerial photography and <37% for satellite imagery.

Over the last 20 years, the various types of remote sensing have complemented each other. Advances in the analysis techniques for digitized aerial photography has largely come from satellite imagery (see Andrefouet and Riegl, 2004), and sophisticated airborne scanners have combined the advantages of these complementary techniques. Coral reef science has benefitted from remote sensing for almost 100 years. Among all the aerial remote sensing techniques, aerial photography still has the finest resolving power. For example, further experiments by Hopley and Catt (1988) on Cape Tribulation reefs (GBR) used photography from as low as 500' (152 m), producing images with a pixel size of only  $7 \times 7$  cm, sufficient to differentiate between major groupings of corals and other organisms. The main disadvantage is the size of the data bank resulting from the very high resolution. Nonetheless, aerial photography remains an important tool for documenting the physical and ecological complexity of coral reef habitat, especially when the scale and resolution are geared to the specific needs of the project with which it is associated (see also *Remote Sensing*).

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## Cross-references

[Remote Sensing](#)

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## AGASSIZ, ALEXANDER (1835–1910)

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Alexander Agassiz was born on 17 December 1835 in Neuchâtel, Switzerland. He was the son of the famous naturalist Louis Agassiz. A. Agassiz made a distinguished

career as reef scientist, zoologist, mining engineer, and science administrator in the US (Dobbs, 2005). After receiving a degree in engineering and chemistry, he studied biology at Harvard University from 1865 to 1869. Since 1860, Agassiz had been working at the Museum of Comparative Zoology as an assistant and since 1875 as curator. His field was marine invertebrates and he was especially interested in echinoderms, annelids, cnidarians, and coral reefs. Interestingly, starting in 1865, Agassiz made a second career in mining because he had inherited the Calumet Copper Mine in Michigan. Eventually, he became one of the richest Americans and financed his own research expeditions starting in mid-1870ies, which led him to almost every major reef area on earth. Expeditions went to Florida, the Bahamas, Bermuda, Cuba, the Yucatán, Galápagos, Hawaii, Fiji, Tonga, the Ellice Islands (now: Tuvalu), Marshall Islands, Gilbert Islands, Caroline Islands, the Tuamotus, Cook Islands, Guam, Japan, the Maldives, and the Great Barrier Reef. He published six major monographs on reefs (Agassiz, 1885, 1889, 1894, 1899, 1903a, b) and numerous shorter papers. A summary of his work can be found in two relatively brief but instructive articles (Agassiz, 1900, 1903c). Agassiz was a follower of the Murray (1889) theory proposing that reefs grew from a submarine plateau to the water surface, opposing Darwin's (1842) subsidence theory. He proposed that denudation and submarine erosion can create shallow platforms from which reefs can accrete. For example, the Maldives archipelago was used by Agassiz in support of this model. Some barrier reef lagoons were formed through erosion, e.g., in the Society Islands, Fijis, Carolines, according to Agassiz. He also considered moderate recent uplift as important agent of modern reef formation, e.g., in the Tuamotu archipelago. When summarizing his observations on reefs, Agassiz erred in interpreting exposed limestone as well as shallow submarine rock ledges as remnants of denuded and eroded fossil (Tertiary) limestone. Much later, many of these outcrops and submarine terraces were radiometrically dated and turned out to be of late Quaternary age. Even so, Agassiz's observations on reefs worldwide served as a basis for numerous later studies, and, he critically challenged Darwin's subsidence theory thereby stimulating subsequent research that identified the importance of factors such as erosion and sea-level change for reef development. After being a curator in Harvard for 23 years, Agassiz became the head of the Museum of Comparative Zoology for 10 years. He also served as President of the US National Academy of Science for 6 years (1901–1907). A. Agassiz died on 23 March 1910 aboard a ship sailing from Southampton to New York.

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- Darwin, Charles (1809–1882)
- Gardiner, John Stanley (1872–1946)
- Reef Classification by Fairbridge (1950)
- Reef Classification by Hopley (1982)
- Reef Classification by Maxwell (1968)
- Subsidence Hypothesis of Reef Development

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## AIRBORNE DUST IMPACTS

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### Definition

As in the Dust Bowl of the Midwestern United States in the 1930s, arid-soil conditions exist in other countries today. Periodically, ground-level winds associated with high-energy fronts, pick up the soils along with whatever chemical or pollutant may be associated with the source soil and lift them into the troposphere. Wind systems such as the trade winds transport the dust clouds with their exotic components around the globe. Impacts of these airborne dusts are just now being recognized. Many of the non-soil substances such as pesticides are known to be toxic to human health, marine life, and coral reef ecosystems.

### Background

Soil dust (generally less than 10  $\mu\text{m}$  in diameter) containing viable microbes, toxic minerals, radiogenic elements, feces, and modern pesticides may negatively impact corals and coral reef-associated organisms as well as human health and terrestrial ecosystems. Marine impacts from this noxious mix are likely to be most pronounced in pristine clear-water areas, where corals have not previously adapted to stressors such as nutrients, pollution, and sedimentation.

In recent years beginning in 1973, the changing climate and desertification of the North African Sahel region resulted in increased quantities and ongoing transport of soil dust to the Americas (Prospero and Nees, 1986). Shinn et al. (2000) summarized the relation between annual variations in dust flux and coral demise. Iron, the most consistent elemental component of soil dust, after silica, has been shown to stimulate red-tide outbreaks in the Gulf of Mexico (Walsh et al., 2006). Red-tide outbreaks can have devastating effects on coral reefs.

The quantity of soil dust leaving Africa each year has been estimated to be as high as 1 billion tons (D’Almeida, 1986). Hundreds of millions of tons reach Caribbean reefs and the Amazon rainforest annually (Prospero et al., 1996).

### Processes

African dust periodically impacts the entire East Coast of the US and occasionally exceeds Environmental Protection Agency atmospheric-particulate standards in Miami, Florida (Prospero, 1999). African dust has been transported as far west as Carlsbad, New Mexico (Perry et al., 1990). During Northern Hemisphere winters, African dust storms shift southward with the Intertropical Convergence Zone (ITCZ) and are known to be a major supplier of nutrients to the Amazon Basin (Swap et al., 1992).

During Northern Hemisphere summers, the ITCZ shifts northward, creating conditions conducive to dust storms and subsequent transport of dust and adhering contaminants across the Atlantic Ocean. The same weather conditions are responsible for creation of Atlantic hurricane formation, especially the so-called Cape Verde storms that originate late in the season.

African dust storms initiate when strong winds lift soil from dried lakebeds, especially in the Bodele Depression, located in Chad in central Africa (Koren et al., 2006). Once airborne, the dust is carried by trade winds in the troposphere (below 3,000 m) in what meteorologists call the Saharan air layer. Dust clouds leaving northwest Africa typically reach the Americas in 5–7 days. Recent and ongoing studies indicate African dust storms retard or prevent hurricane formation by suppressing raindrop formation and precipitation, while at the same time shading sunlight and cooling sea-surface waters. Dust storms also create hazy days and beautiful sunsets.

Dust-borne winds occur at irregular intervals. Peak formation and transport are associated with positive phases of the North Atlantic Oscillation (NAO). The NAO is the difference between pressure at the Azores High (sometimes called the Bermuda High) and the Icelandic Low. The NAO is dependent on the route and intensity of the trade winds. During positive NAOs, this persistent barometric high drifts eastward, closer to Africa where it alters meteorological conditions and suppresses rainfall. Positive phases of the NAO thus induce droughts. The NAO is also linked, and influenced, by the much larger El Niño



Southern Oscillation (ENSO). The ENSO has worldwide meteorological effects, including increasing wind shear in the subtropical Atlantic that is also known to suppress tropical-cyclone formation.

## Effects

Iron and minerals in African dust form reddish-brown layers in white- to cream-colored carbonate sediments throughout the rock record in Florida and the Caribbean. In modern times, Caribbean corals experienced an unusual onset of disease and demise in the late 1970s that peaked in 1983–1984. The peak coincided with a major ENSO and positive NAO coupled with the largest dust flux at the island of Barbados since monitoring began there in 1965 (Shinn et al., 2000). Significant coral bleaching began in the Pacific in 1982–1983 (Glynn, 1988), followed by widespread Atlantic coral bleaching in 1986–1987, both times of high dust flux. The El Niño of 1998 was also a time of increased dust flux to the Caribbean.

Sporadic fish kills and cases of ciguatera fish poisonings occurred in 1983–1984. Caribbean-wide demise of the herbivorous black long-spined sea urchin *Diadema antillarum* (Lessios et al., 1984) and onset of sea-fan disease caused by the soil fungus *Aspergillus sydowii* also began around that time (Weir-Brush et al., 2004). *Aspergillus sydowii* has been cultured from African dust collected in Mali, Africa. *Aspergillus sydowii* does not reproduce in seawater. These Caribbean-wide die-offs severely impacted reef vitality by allowing algal growth to go unchecked. Whether diseases and bleaching are caused by specific elements or microbes carried by African dust or simple elevation of water temperature is controversial and not well understood. A major problem has been separating effects of dust from those of the rising temperature. Both hypotheses are based mainly on correlation and not on absolute proof, other than the fact that *A. sydowii* is a verified cause of sea-fan disease.

What is known is that viable microbes, bacteria, and fungi are common dust components (Griffin et al., 2003; Griffin, 2007). Shielding of ultraviolet radiation by the dust clouds themselves enables microbes to survive long journeys through the atmosphere. Hundreds of viable species have been cultured and recognized in dust thus far (Kellogg and Griffin, 2006). Of those recognized, about 10% are human pathogens and 30% are plant pathogens (Griffin et al., 2003). Most microbes recovered from dust have not yet been identified.

In addition to viable microbes, toxic metals including mercury and arsenic are also components of dust (Holmes and Miller, 2004; Garrison et al., 2006). Bioassays have shown that copper in African dust is toxic to phytoplankton in near-surface ocean waters and thus affects primary productivity as well as the CO<sub>2</sub> budget (Payton et al., 2009). Human-health effects, first noted by Darwin (1845) while he was aboard the HMS *Beagle*, are well known to Caribbean-island citizens.

## Asian dust

Asian and Australian dusts settle on Pacific and Indian Ocean coral reefs and atolls but effects of those dusts are less well known. Australian dust contains abundant microbes (De Deckker, 2008). In addition, red tides have been reported along the Australian coast following dust events. Satellite imagery shows that Australian dust clouds usually move from the west (Outback region) out over the Great Barrier Reef and eastward toward New Zealand.

Beginning in April, Asian dust clouds often blanket Korea, pass over Japan, and then cross the North Pacific. Iron in Asian dust increases primary productivity in the open Pacific (Young et al., 1991). Asian dust is also the source of soils in the Hawaiian Islands (Chadwick et al., 1999). These dust clouds impact the Western US, Alaska, and the North Sea where the dust stains sea ice. Asian dust has at times blocked the sun in Denver, Colorado, and has been identified, along with African dust, in Alpine snow. Asian dust is widespread, yet there are few published accounts of its toxic components, especially microbes. Clearly, Asian dust transports industrial pollutants as it passes over Chinese factories and coal-fired power plants. The full effects of Asian dust on coral reefs in the Pacific and Indian Oceans are not well known. Investigation of impacts of various airborne soil dusts on coral reefs and other marine organisms is in its infancy.

## Summary

Dust storms are global events. Dusts from Africa, Asia, the Americas, the Middle East, and Australia periodically fill the air with soil particles to which viable microbes, bacteria, fungi, and toxic chemicals are attached. Dusts and their exotic components are transported through the troposphere to be deposited far from their sources. Dusts cause hazy days and spectacular sunsets, but also pose risk to human health (e.g., asthma), marine life (e.g., red tides), and coral reef health (e.g., sea-fan disease). Impacts of airborne dusts on all ecosystems are just beginning to be recognized.

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## Cross-references

Bahamas  
 Climate Change: Increasing Storm Activity  
 Darwin, Charles (1809–1882)  
 El Niño, La Niña, and ENSO  
 Florida Keys  
 Heavy Metal Accumulation in Scleractinian Corals  
 Indian Ocean Reefs  
 Microbes  
 Pacific Coral Reefs: An Introduction  
 Temperature Change: Bleaching  
 Western Atlantic/Caribbean, Coral Reefs

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## ALGAE, BLUE-GREEN BORING

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## Synonyms

Blue-green microborers/endoliths; Endolithic (euendolithic) cyanophyta/cyanobacteria; Rock-boring blue-green algae

## Definition

The blue-green boring algae are filamentous, prokaryotic, mostly photosynthetic organisms that chemically bore into calcareous rock and limestone.

Penetrating or boring algae play important roles in the bioerosion of coral reefs; these filamentous microorganisms result in the breakdown of carbonate structure both directly and indirectly [see Tribollet (2008) for review]. They occur from the upper intertidal to abyssal depths (Golubic et al., 1984), but, in general, show a decrease with depth. The commonest are blue-green algae (Cyanophyta, Cyanobacteria) that attack calcareous substrates differentially; the aragonite skeletons of corals are most easily penetrated and the denser calcite deposits of coralline algae are most resistant. However, the mechanism of carbonate dissolution remains largely unknown and actually contradicts geochemical models that predict the precipitation of carbonates by photosynthetically induced pH increases. As a consequence of variable processes, such as selective settling, competition, persistence, and subsequent grazing of euendolithic (true endoliths) Cyanobacteria, coastal rocks are biodegraded differentially, resulting in grotesque sharp-edged features called karsts (Figure 1). These processes act as feedback mechanisms by producing diverse microbial habitats with patchy water-retention pockets, which further enhance bioerosion and endolithic community diversity.

Boring endoliths colonize all carbonate substrates on coral reefs and are distributed throughout the world's tropical seas. Intertidal carbonate coasts are most intensively bioeroded (Figure 2). However, endolithic activity not only negatively inflicts damage to living hosts, but also





**Algae, Blue-Green Boring, Figure 1** Example of karsts formed by irregular habitats colonized by boring Cyanobacteria and their deeply rasping predators.



**Algae, Blue-Green Boring, Figure 2** Example of boring blue-green algal intertidal zone mostly undercut by deep-rasping chitons.

can provide positive overall benefits to reefs as well, including important primary productivity yields in otherwise dead substrates. Endoliths attract excavating grazers (Figures 3 and 4), which contributes to massive biodestruction processes and sediment formation. In other words, the bioerosional effect of boring Cyanobacteria alone is secondary; their primary significance is in providing the nutritional base for excavating grazers.

Boring Cyanobacteria have been important in the destruction of carbonate, throughout geological times. Marine limestones can be infiltrated by more than 0.5 million endolithic filaments per square centimeter. The oldest recorded endolithic blue-green was found from 1.5 billion-year-old stromatolite rocks in China (Zhang and Golubic, 1987) – the earliest known occurrence of bioerosion.



**Algae, Blue-Green Boring, Figure 3** Chitons rasping deep holes in the intertidal substrate.



**Algae, Blue-Green Boring, Figure 4** Gastropods taking shelter in sharp karst formed by these excavating grazers.

The diversity of boring micro flora is thought to be large, comprising not only undiscovered blue-green algae, but also including other algae (chlorophytes, rhodophytes) and fungi. Although their taxonomy has been studied for decades, new species are still being discovered, especially following the advent of molecular techniques. However,

the taxonomy and diversity of boring blue-green algae remain relatively unknown.

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## Cross-references

[Stromatolites](#)

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## ALGAE, CORALLINE

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## Synonyms

Calcareous Corallinales; Corallines; Coralline algae; Nullipores; Rhodalgal facies (geological term)

## Definition

Coralline algae are heavily calcified red algae of the order Corallinales (Rhodophyta). The plant body (thallus) is composed of chains of cells (filaments) that may fuse laterally or also form secondary (lateral) pit connections. Separate haploid male and female plants produce gametes in sori (spore clusters) or domed single-pored conceptacles, with spores (haploid tetraspores or diploid bispores) being formed in sori that are typically modified into either single-pored or multipored conceptacles.

## Introduction

Coralline algae are important carbonate sediment producers and rank among the major reef builders. Corallines are characterized by a thallus that is stony because of calcareous deposits contained within and between the cell walls. This extensive calcite crystalline form of  $\text{CaCO}_3$  is a major factor determining the geological importance of the group. High preservation potential has produced an excellent fossil record. The colors of these algae are most typically pink or other shade of red, but some species can be variations of purple, blue, gray-green, or brown. Beginning with their discovery in 1707 (Sloane), corallines were thought to be animals. However, in 1837 Philippi recognized that coralline algae were plants and

proposed the two generic names *Lithophyllum* (for flat forms) and *Lithothamnium* (for erect branched forms). However, in an overlooked earlier treatment, Bory de Saint-Vincent (1832) had recognized *Tenarea undulosa* as a crustose calcareous alga, making it the oldest species name originally applied to the coralline algae in a botanical context. For many years, coralline algae were included in the Order Cryptonemiales as the Family Corallinaceae until 1986 (Silva and Johansen) when they were elevated to the Order Corallinales.

## Systematics

The Corallinales is a monophyletic group comprised of three Families (Table 1, Sporolithaceae, Corallinaceae, and Hapalidiaceae). They also comprise two very distinct morphological groups [i.e., geniculate (articulated, segmented, jointed) species and nongeniculate (non-articulated, unsegmented, crustose) species]. Though useful, this traditional separation no longer constitutes a phylogenetic arrangement (Bailey, 1999).

## Life history

Coralline algae are exclusively marine plants and occur throughout all of the world's oceans, where they often cover most of the available hard substrates, being attached by crustose expanses (cellular adhesion) or root-like hold-fasts (haustoria). Many are epiphytic (on other plants) or epizoic (on animals), and some are even endophytic parasites within other corallines. Despite their ubiquity, the coralline algae remain poorly understood by coral-reef scientists, and even by specialist algologists/phytologists. Corallines reproduce by sori, which are specialized volcano-shaped domed conceptacles containing haploid tetraspores, diploid bispores, or either male or female gametes. Gametes fuse to form the parasitic diploid carposporophyte stage within the female conceptacles and the resultant carpospores germinate into diploid tetrasporophytes. Haploid tetraspores germinate to produce the male and female gametophytes. Some crustose coralline populations are unusual in that uninucleate bispores (diploid) are commonly the sole means of reproduction. The plant body (thallus) is composed of strands of pit-connected cells (filaments) that may fuse laterally or also form secondary pit connections. Pit connections and pit plugs are translocational structures characteristic of red algae (Rhodophyta). These reproductive and vegetative structures provide the critical anatomical characters used in coralline algal taxonomy, but also create major obstacles for workers, since complicated decalcification techniques and microtome sectioning of infrequently present cryptic features are required.

Articulated (geniculate) corallines are upright or pendulous branched bushy plants (Figure 1), with shallower and warmer distributions than nongeniculate species. The multiple clumped thalli are flexible due to noncalcified zones (genicula, joints) separating longer



**Algae, Coralline, Table 1** Classification (families, subfamilies, genera, and authors) of the Order Corallinales (modified from AlgaeBase.org, 2009)

|                                                                                          |
|------------------------------------------------------------------------------------------|
| Sporolithaceae (each cruciate tetrasporangium borne in a single sorus)                   |
| Sporolithoideae                                                                          |
| <i>Sporolithon</i> Heydrich                                                              |
| <i>Heydrichia</i> Townsend, Y.M. Chamberlain & Keats                                     |
| Corallinaceae (multiple zonate tetrasporangia borne in unplugged uniporate conceptacles) |
| <i>Fosliella</i> M.A. Howe                                                               |
| <i>Goniolithon</i> Foslie                                                                |
| <i>Heteroderma</i> Foslie                                                                |
| <i>Litholepis</i> Foslie                                                                 |
| <i>Porolithon</i> Foslie                                                                 |
| <i>Pseudolithophyllum</i> Lemoine                                                        |
| Lithophylloideae                                                                         |
| <i>Ezo</i> Adey, Masaki, & Akioka                                                        |
| <i>Lithophyllum</i> Philippi                                                             |
| <i>Paulsilvella</i> Woelkerling, Sartoni, & Boddi                                        |
| <i>Tenarea</i> Bory de Saint-Vincent                                                     |
| <i>Titanoderma</i> Nägeli                                                                |
| Mastophoroideae                                                                          |
| <i>Hydrolithon</i> (Foslie) Foslie                                                       |
| <i>Lesueuria</i> Woelkerling & Ducker                                                    |
| <i>Lithoporella</i> (Foslie) Foslie                                                      |
| <i>Mastophora</i> Decaisne                                                               |
| <i>Metamastophora</i> Setchell                                                           |
| <i>Neogoniolithon</i> Setchell & Mason                                                   |
| <i>Pneophyllum</i> Kützing                                                               |
| <i>Spongites</i> Kützing                                                                 |
| Amphiroideae                                                                             |
| <i>Amphiroa</i> J.V. Lamouroux                                                           |
| <i>Lithothrix</i> J.E. Gray                                                              |
| Corallinoideae                                                                           |
| <i>Alatocladia</i> (Yendo) Johansen                                                      |
| <i>Arthrocardia</i> Decaisne                                                             |
| <i>Bossiella</i> P.C. Silva                                                              |
| <i>Calliarthron</i> Manza                                                                |
| <i>Chiharea</i> Johansen                                                                 |
| <i>Cheilosporum</i> (Decaisne) Zanardini                                                 |
| <i>Corallina</i> Linnaeus                                                                |
| <i>Dermatolithon</i> Foslie                                                              |
| <i>Halptilon</i> (Decaisne) Lindley                                                      |
| <i>Jania</i> J.V. Lamouroux                                                              |
| <i>Marginisporum</i> (Yendo) Ganesan                                                     |
| <i>Pachyarthron</i> Manza                                                                |
| <i>Rhizolamiella</i> Scheveiko                                                           |
| <i>Serraticardia</i> (Yendo) P.C. Silva                                                  |
| <i>Yamadaea</i> Segawa                                                                   |
| Metagoniolihoideae                                                                       |
| <i>Metagoniolithon</i> Weber-van Bosse                                                   |
| Hapalidiaceae (multiple zonate tetrasporangia borne in plugged multiporate conceptacles) |
| Austrolithoideae                                                                         |
| <i>Austrolithon</i> A.S. Harvey & Woelkerling                                            |
| <i>Boreolithon</i> A.S. Harvey & Woelkerling                                             |
| <i>Epulo</i> R.A. Townsend & Huisman                                                     |
| Choreonematoideae                                                                        |
| <i>Choreonema</i> F. Schmitz                                                             |
| Melobesioideae                                                                           |
| <i>Clathromorphum</i> Foslie                                                             |
| <i>Exilicrusta</i> Y.M. Chamberlain                                                      |
| <i>Kvaleya</i> W.H. Adey & Sperapani                                                     |

**Algae, Coralline, Table 1** (Continued)

*Leptophytum* W.H. Adey  
*Lithothamnion* Heydrich  
*Mastophoropsis* Woelkerling  
*Melobesia* J.V. Lamouroux  
*Mesophyllum* Lemoine  
*Phymatolithon* Foslie  
*Synarthrophyton* Townsend

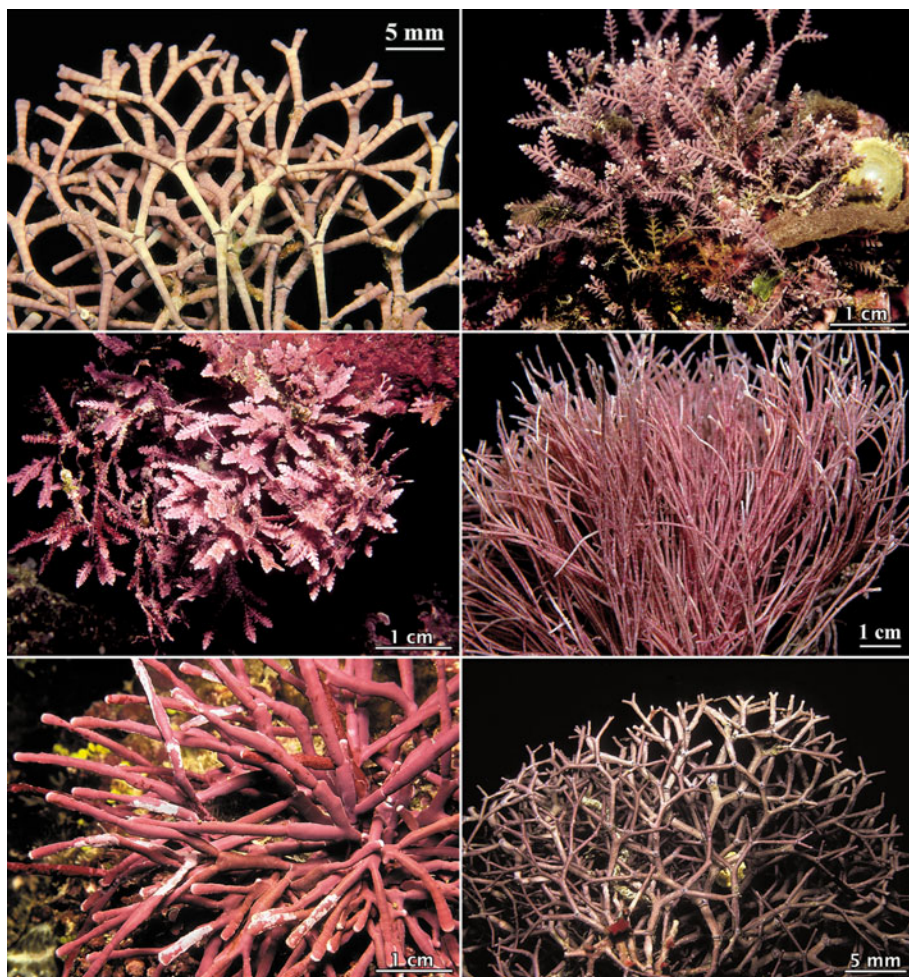
calcified segments (intergenicula). Many articulated and upright crustose corallines can also form extensive two-dimensional adherent crusts, allowing them to spread laterally, thereby providing those species with multiple “bet-hedging” ecological survival strategies (called heterotrichy; Littler and Kauker, 1984). The upright portions receive relatively more light and nutrients, and are faster growing with increased fertility; whereas, horizontal crusts are more resistant to physical forces such as grazing, wave shearing, and sand scouring, while allowing the plants to invade horizontal primary space.

Crustose (nongeniculate) corallines range in thickness from a few micrometers to many centimeters (Figures 2 and 3). The thinner forms are faster-growing early colonizers and occur on all hard substrates and other marine organisms. Crustose corallines span a spectrum of morphotypes from thin sheet-like crusts to thick slow-growing massive pavements to upright branched and columnar coral-like heads that contribute to both cementation and bulk. On oceanic reefs, the highest part of the reef is often a massive “algal ridge” of crustose corallines in the reef’s breaker zone (Dawson, 1961) – see below. Thalli of thicker forms often consist of three recognizable layers: an attached lower hypothallus, a middle perithallus, and an upper epithallus. Trichocytes (hair cells, megacells) occur as horizontal plates within the epithallus layer in some genera such as *Porolithon*. The meristematic (growing) region is usually located as a layer beneath the uppermost intercalary perithallus cells, a feature which is unusual in the Rhodophyta, whose members (except also for Delesseriaceae) typically show strictly apical cell growth. Because of the upright branched head formers (Figure 3), some specialists prefer the term nongeniculate over crustose; however, all have extensive crustose bases and whether branched or simple they are still elaborations of crusts.

### Rhodoliths

In the absence of hard substrates, many nongeniculate species can propagate as free-living rhodolith nodules colonizing sedimentary seafloors (Figure 4). Some of the attached crustose corallines break free and then continue spherical growth as they are tumbled by wave action and bioturbation to ultimately cover vast areas as free-living rhodoliths (= nodules, rhodolites, maërl, red algal balls, algaliths). Rhodolith beds have been found throughout



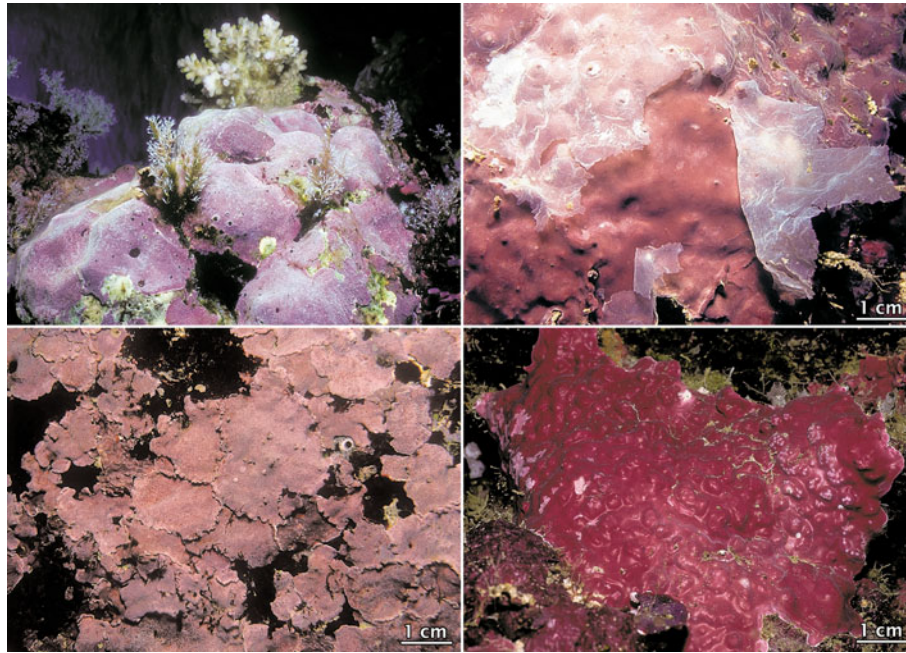


**Algae, Coralline, Figure 1** Spectrum of articulated (jointed, geniculate) coralline algal forms.

all of the world's oceans. Globally, rhodoliths fill an important niche in marine ecosystems, serving as transitional habitats between rocky substrates and barren sedimentary areas. Under favorable preservation conditions, rhodoliths can be the predominant contributors of carbonate sediments, often forming rudstone or floatstone depositional beds consisting of large fragments of rhodoliths contained in grainy matrices. Although they are rolled by infrequent storms, rhodoliths nevertheless provide a three-dimensional micro-habitat onto which a wide variety of species attach, including other algae, corals, and commercial species such as clams, oysters, and scallops. Rhodoliths are a common feature of modern and ancient carbonate shelves worldwide. Fossil rhodoliths commonly are used to derive paleoecological and paleoclimatic information and rhodolith communities contribute significantly to the global calcium carbonate budget.

Quantitative submersible studies (Littler et al., 1991) of deep-water rhodolith development, distribution,

abundance, and primary productivity, at sites of both active formation and breakdown, provided the following detailed case-study. The 1.27 km<sup>2</sup> upper platform (67–91 m deep) of a ~1,000-m high Bahamian seamount (San Salvador Seamount) averaged 95.8% cover of rhodoliths, contributing an impressive 391 tons of organic carbon per year to deep-sea productivity (tropical storms cause the rhodoliths to roll at this depth). The predominant crustose coralline alga was acclimated to extremely low light ranges, with an extremely narrow PI curve (photosynthesis vs. irradiance) of net primary productivity (0.005 to slightly beyond 0.24  $\mu\text{mol}$  per meter square per sec of photosynthetically active radiation). Horizontal platform areas contained up to five-deep accumulations (about 45 cm thick) of rhodoliths, with their visible planar (two-dimensional) crustose algal cover (68.5%) being composed of 41% *Lithophyllum* sp., 14.9% mixed crustose corallines, and 12.6% *Peyssonnelia* sp. The platform rhodoliths also contained an average 25% cover of the



**Algae, Coralline, Figure 2** Spectrum of simple two-dimensional forms of nongeniculate (crustose) corallines. *Upper right* image shows synchronous sloughing in *Neogoniolithon fosliei*.

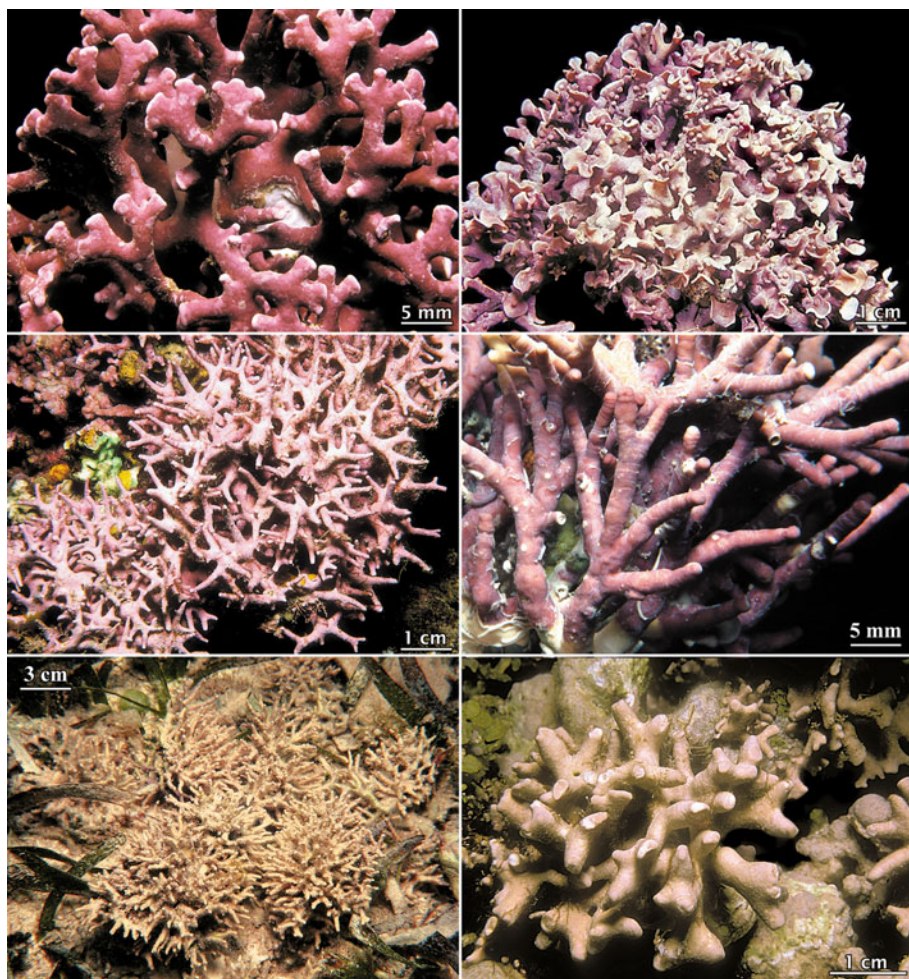
foraminiferan *Gypsina* sp.: by contrast, *Gypsina* cover was minimal on the slope rhodoliths. Rhodoliths that had spilled down from the relatively flat platform tended to be concentrated in fan-shaped deposits that were more prevalent near the tops of the slopes. Cover of living crustose algae on the deeper slope rhodoliths averaged only 22.8% and was made up of 14.8% unidentified crustose corallines, 6% *Lithophyllum* sp., and 2% *Peyssonnelia* sp.

Throughout platform depths from 67 to 91 m, rhodoliths were fairly uniform in composition and abundance. They ranged from 4 to 15 cm in diameter, with an average diameter of about 9 cm, and were roughly spherical with smooth living surfaces. The rugose rhodoliths spilling down the steep slopes of the seamount to depths below 200 m were characteristically smaller (mean of about 5 cm diameter), much rougher, and pitted by boring organisms. Cross-sections through the centers of upperplatform nodules showed outer relatively thin (1–3 cm thick) well-preserved envelopes overlying dead laminated crustose layers). These layers surrounded much thicker cores of biotically altered carbonates (comprised mostly of corallines, foraminiferans, and corals) that had been extensively reworked by boring sponges, boring algae, polychaetes, and pelecypods. Radiocarbon dating indicated that the outermost unaltered envelopes beneath actively growing crusts averaged 429 years old (range = 112 to 880 ybp), while the innermost unaltered layers showed a mean age of 731 ybp (200–1,100 ybp).

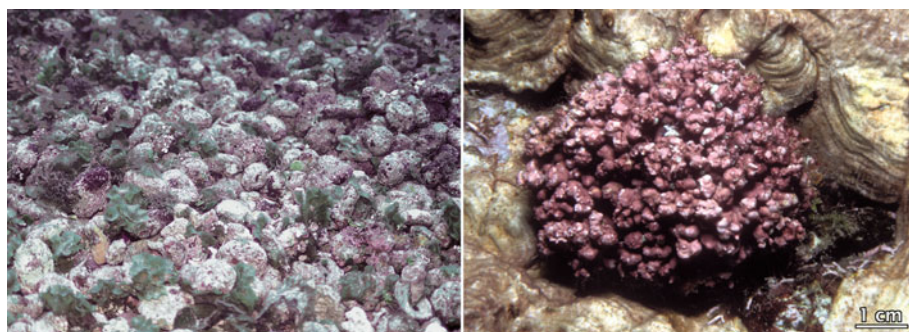
## Geology and evolution

Crustose coralline algae appeared in the early Cretaceous and have been important components of shallow-marine communities throughout the Cenozoic, mostly showing long-term increases in species richness during much of their history. There are currently over 1,600 described species of crustose coralline algae (Woelkerling, 1988) and ~649 fossil species (Aguirre et al., 2000). Interestingly, Miocene coastal carbonate habitats are characterized by a worldwide bloom of coralline red algal deposits (termed rhodalgal facies). These extensively developed facies (i.e., characteristic sedimentary deposits) temporarily replaced corals throughout the tropics and subtropics as dominant carbonate producers (e.g., Esteban, 1996). By calibrating modern carbonate assemblages to local oceanographic conditions in the Gulf of California, Halfar et al. (2004) demonstrated that the predominance of rhodalgal facies occurred under mesotrophic to slightly eutrophic conditions. In the Mediterranean region, early to middle Miocene carbonates contain more rhodalgal components than coral-reef deposits (Esteban, 1996). In addition to being widespread globally, fossil coralline algae also exhibited their greatest species richness during the early and middle Cenozoic (early Miocene peak of 245 species; Aguirre et al., 2000), with a collapse to a late Pleistocene low of 43 species. In reviewing 37 representative late Pliocene studies, Halfar and Mutti (2005) concluded that although rhodalgal facies were clearly the dominant components at specific study sites, they often were not





**Algae, Coralline, Figure 3** Spectrum of head-forming crustose corallines with upright branched excrescences.



**Algae, Coralline, Figure 4** Examples of coralline algal rhodoliths.

emphasized as extensively as the much better-known coral assemblages. A number of the above studies focused mainly on coral-reef components; whereas, rigorous reanalyses of the facies studied actually indicated a relatively low percentage of corals and a predominance of rhodoliths. Esteban (1996) noted a similar bias in

a review of Miocene Mediterranean coral reefs and rhodalgal facies. Such discrepancies can be attributed mostly to poor knowledge of coralline red algae and rhodolith facies, in conjunction with the tendency for workers to apply classic coral-reef depositional models, even in settings where corals were sparse.



Throughout the world's oceans, during the late/early to early/late Miocene, while many phototrophs declined globally, coralline red algae radiated and diversified greatly. In fact, corallines have shown a long-term overall increase in species richness throughout most of their history. Despite this, coralline species diversification was not sustained after the Miocene (Aguirre et al., 2000) and coralline algae suffered a series of extinction events, each of which eliminated at least 20% of the species. In fact, during the two largest extinction events of the late Cretaceous and late Miocene-Pliocene, about 66% of all coralline species were lost. Each extinction event was followed by substantial episodes of rapid radiation and speciation, particularly in the early Paleocene and Pleistocene.

The conspicuous Miocene shift from coral- to rhodolith-dominated carbonate communities has been attributed to global climate changes. Halfar and Mutti (2005) argued that the prevalence of rhodolith facies, which developed under broader nutrient and temperature ranges than did the coral-reef facies, was initially triggered by a global enhancement of nutrient resources. In the middle Miocene, nutrient availability was apparently augmented by increased upwelling- and erosion-related nutrient inputs into coastal ecosystems. These nutrient increases together with declining temperatures, following the early to middle Miocene climatic optimum, led to further expansion of rhodalgial facies. Hence, a global phase shift occurred in nearshore shallow-water carbonate producers from corals to domination by coralline species that were tolerant of the higher levels of nutrification. Geological deposits of coralline algae contain organic carbon compounds such as cellulose (due to photosynthesis) as well as massive calcareous compounds due to calcification (precipitation of inorganic  $\text{CaCO}_3$ ). The resultant carbon stores may be among the most important in the biosphere as neutralizers of global oceanic acidification and as reservoirs of excess greenhouse  $\text{CO}_2$ .

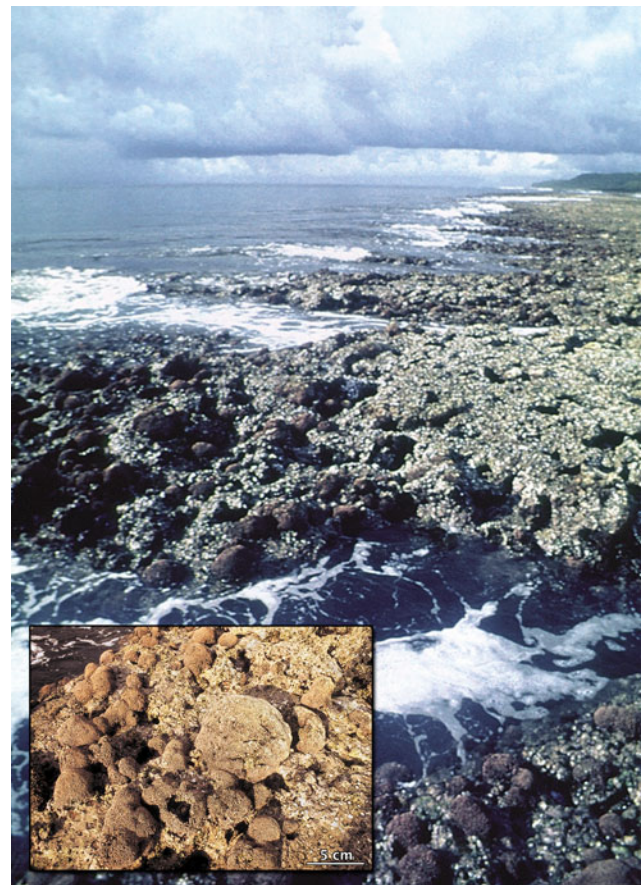
A striking geological pattern is the occurrence of an inverse relationship in the species richness of two of the families of Corallinales. From the Cretaceous to Pleistocene, Corallinaceae (both warm- and cold-water species) increased, while the tropical Sporolithaceae declined. This climatic link was supported for Sporolithaceae and Corallinaceae by both direct and inverse correlations, respectively, between species diversity and documented Cretaceous to Cenozoic paleotemperatures. Although, remaining to be more firmly established, coralline diversification since the Cretaceous (Steneck, 1983, 1985) may have been driven by simultaneous coevolutionary increases in herbivores (mainly limpets, echinoids, and grazing fishes) that physically scrape and remove fleshy algal competitors.

### Distribution patterns and functional significance

Crustose (nongeniculate) coralline algae occur worldwide from polar to tropical regions, reaching their highest

diversity in tropical reef environments. Three subgroups of Corallinales show characteristic distributions (Aguirre et al., 2000): (1) Sporolithoideae, low latitude/mainly deepwater; (2) Melobesioideae, high latitude/shallow waters to low latitude/deep waters; and (3) Lithophylloideae/Mastophoroideae, mid to low latitude/shallow waters.

The abundant occurrence of crustose corallines (and corals) in Indo-Pacific reefs was initially recognized by Darwin (1842); however, their important role as reef builders was first emphasized by Agassiz (1888). Most often, corals (Cnidaria) supply the bulk building blocks; whereas, coralline algae do much of the cementing together of debris. Barrier, fringing, and atoll reefs are complex ecosystems that depend on calcareous coralline algae for the development and maintenance of wave-resistant outer fronts (Figure 5). The crustose coralline algae, which deposit a type of calcium carbonate (calcite limestone) that is harder and denser than the aragonite of corals, build this raised "algal ridge" (Dawson, 1961). The intertidal outer algal-ridge habitat, in which crustose



**Algae, Coralline, Figure 5** An example of a well-developed algal ridge from windward Guam, with close-up of the head-forming *Lithophyllum kotschyianum* and the pink crustose *Hydrolithon* (*Porolithon*) *onkodes*.

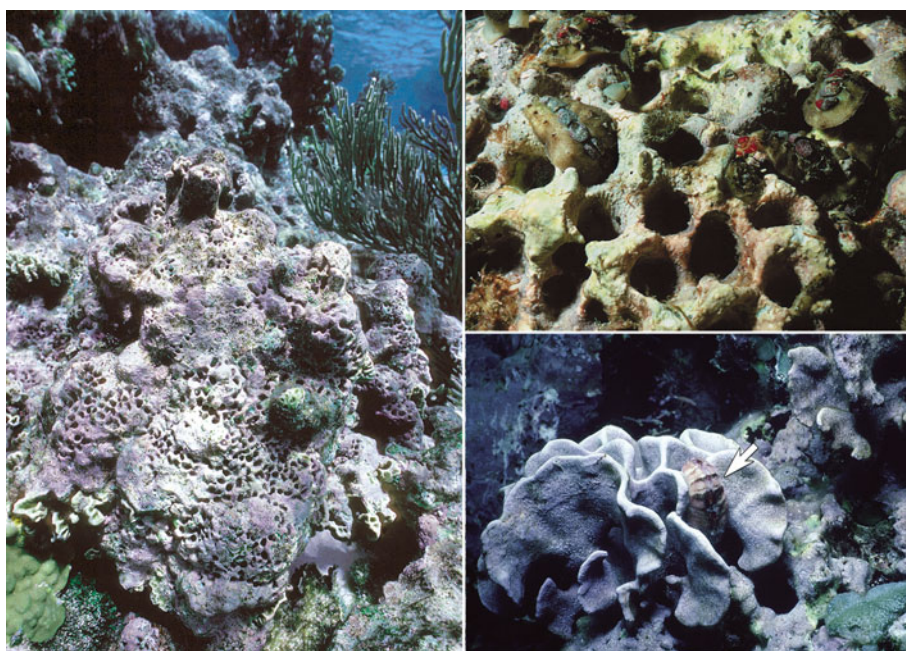
corallines (mainly species of *Hydrolithon*/*Porolithon*) are crucial in constructing the framework, characterizes surf-pounded windward coral reefs of tropical Indo-Pacific and, to a lesser extent, Atlantic regions. The Pacific algal-ridge builder, *Hydrolithon* (*Porolithon*) *onkodes*, fixes a remarkable 3.2 mg of organic carbon per square meter per hour and 1.9 mg Ca per square meter per hour during an average daylight day (Littler, 1973). The algal ridge by extending above the waterline absorbs tremendous wave energy, not only protecting coastal shorelines that would otherwise erode, but also sheltering the more delicate corals and other reef organisms. Algal ridges develop intertidally and, therefore, require intense and persistent wave action to form, so are best developed on windward areas where there are consistent trade wind conditions.

Some of the coralline algae that develop into shelf-like, thick knobby, or upright branched crusts provide microhabitats for countless vulnerable invertebrates that would otherwise suffer increased mortality due to fish predation (Figure 3). Coralline algae also constitute a food source in the energy webs of coral reefs. Sea urchins, parrotfishes, surgeonfishes, limpets, and chitons all readily feed on coralline algae, which are usually not destroyed due to sunken intercalary meristems that replenish the upper damaged areas. Crustose corallines accelerate colonization by chemically attracting/facilitating the survival of coral larvae (Harrington et al., 2004), as well as the larvae of certain grazing invertebrates. This is adaptive for the corallines because the herbivores then remove epiphytes that might preempt available light or otherwise smother

the crusts. Because of their stony texture, indigestible acid-neutralizing  $\text{CaCO}_3$ , and covered intercalary meristematic layer, corallines are uniquely resistant to considerable levels of grazing. As examples, the most common Indo-Pacific crustose coralline, *Hydrolithon* (*Porolithon*) *onkodes*, often forms an intimate interrelationship with the chiton *Cryptoplax larvaeformis* (Littler and Littler, 1999), as does the Atlantic coralline *H. pachydermum* and the chiton *Choneplax lata* (Littler et al., 1995). The chitons live in burrows that are overgrown by *Hydrolithon*/*Porolithon* and graze nocturnally on the surfaces of the corallines (Figure 6). The pattern of grazing causes rapid meristematic differentiation and redirection in which the interaction produces an abundance of vertical blade-like lamellae, resulting in a spectacular growth form (resembling “castles”). This type of relationship is unique in the marine environment – whereby, the predator actually increases the biomass, surface area, and reproductive capacity (i.e., fitness) of its principal prey (Littler et al., 1995).

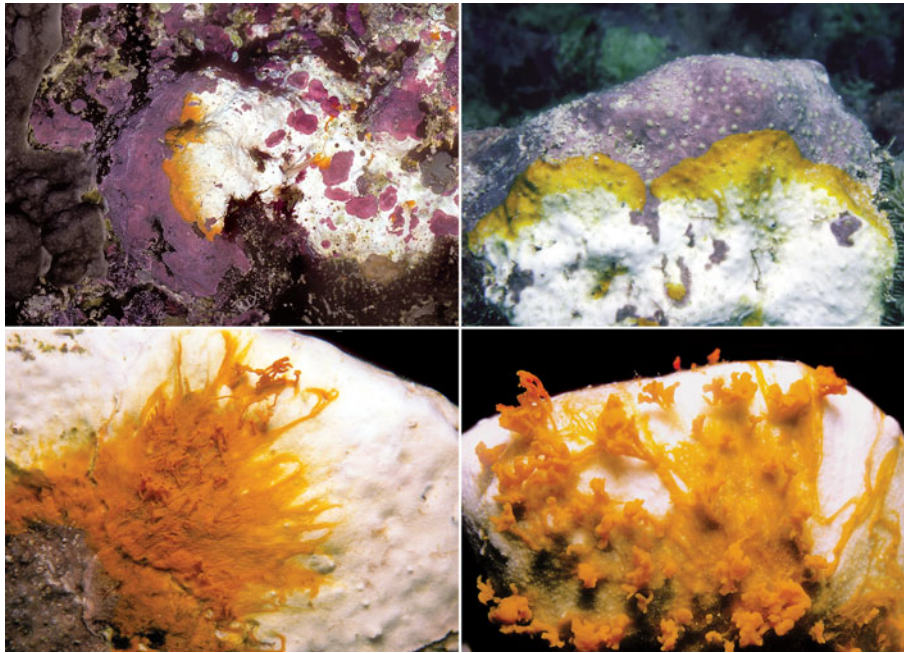
### Pathogens

Instances of coralline algal pathogens were unknown until 1993, when CLOD (Coralline Lethal Orange Disease) was first discovered (Littler and Littler, 1995) on Aitutaki Atoll, Cook Islands (Figure 7). The occurrence of CLOD at 25 Great Astrolabe, Fiji sites increased from 0% in 1992 to 100% in 1993, indicating that the pathogen was in an early stage of virulence and dispersal. The bright orange bacterial pathogen grows as fan-shaped to circular bands at a mean linear rate of increase of 1.5 mm per day,

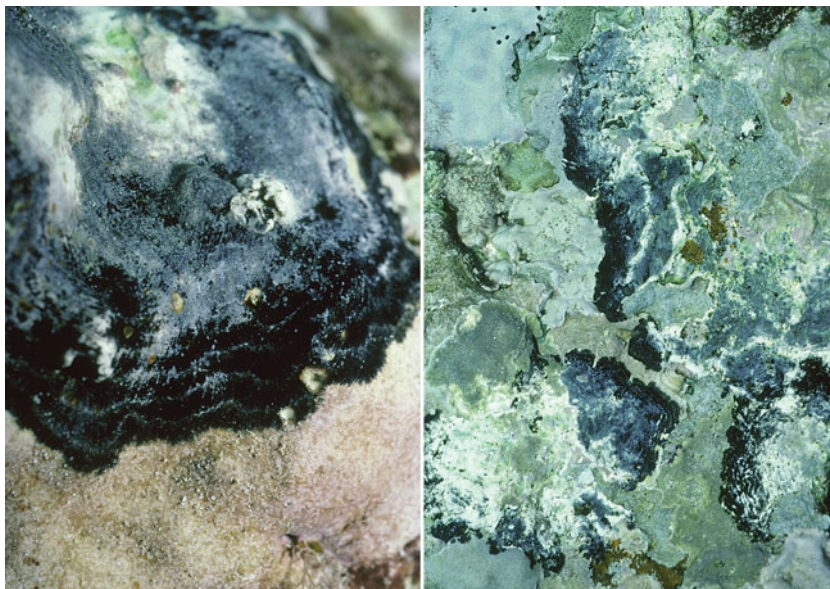


**Algae, Coralline, Figure 6** Castle forms of the crustose corallines created by their association with herbivorous chitons (*Hydrolithon pachydermum*/*Choneplax lata*, left and upper; *H. onkodes*/*Cryptoplax larvaeformis*, lower right).





**Algae, Coralline, Figure 7** In situ images of the worldwide CLOD pathogen.



**Algae, Coralline, Figure 8** In situ images of Black Fungus Disease in the Pacific.

totally consuming host corallines that are left in its wake. All species of articulated and crustose species tested to date are easily infected by CLOD and it has now spread to become circumtropical throughout all coral-reef habitats. In recent years, a white version of CLOD-like pathogen has become even more abundant worldwide, in addition to the recently recorded dispersion of a virulent black fungal pathogen (Figure 8) of coralline algae first

found in American Samoa (Littler and Littler, 1998) and an unknown species of “target-shaped” coralline pathogen (Figure 9), first reported from the Great Astrolabe Reef (Littler et al., 2007).

### Summary

Coralline algae occupy the entire depth range inhabited by photosynthetic organisms; from upper-intertidal regions





**Algae, Coralline, Figure 9** In situ images of Target Pathogen in the Pacific.

to depths as great as 274 m (Figure 10, Littler and Littler, 1994). The great abundances of corallines in the poorly known deep-sea realm underscore their widespread contributions to productivity, the marine food web, sedimentology, and reef biogenesis in clear tropical seas. The diversity of coralline algal forms is astonishing, ranging from small filamentous strands to some of the larger and most beautiful head-forming organisms on coral reefs



**Algae, Coralline, Figure 10** Rock taken by submersible from >200 m off San Salvador Seamount, Bahamas showing the deepest crustose coralline.

(Figures 1–3). The predominant members of this functional indicator group (Littler and Littler, 2007) tend to be slow-growing competitively subordinate taxa abundant in most reef systems. As a indicator group they are functionally resilient and able to expedite the recovery/restoration of a particular coral-reef system relatively quickly, given that some thin forms of crustose coralline algae accelerate colonization and chemically attract and facilitate the survival of coral larvae (Harrington et al., 2004); whereas, the other two fleshy-algal functional indicator groups (i.e., turfs, macroalgae) tend to overgrow and inhibit coral settlement and survival. Because most crustose coralline algae continually slough-off upper surface layers (Figure 2), they play a key role in physically preventing the settlement and colonization of many fleshy fouling organisms on coral reefs (Littler and Littler, 1997).

Crustose corallines, because of their slow growth, tolerate a wide-range of nutrient levels and generally are conspicuous, but not as predominant as corals, under low concentrations of nutrients and high levels of herbivory (Littler and Littler, 2007). Accordingly, they do well in the presence of both low and elevated nutrients [i.e., most are not inhibited by nutrient stress and many are maintained competitor-free by surface cell-layer shedding (Johnson and Mann, 1986), even at lower levels of grazing (Littler and Littler, 1997)]. Therefore, crustose coralline algae do not require elevated nutrients as might be inferred

(Littler and Littler, 2007); instead, the degree to which they rise to dominance is largely controlled indirectly by the factors influencing the abundances of other functional groups, primarily the corals and fleshy macroalgae. The key point is that crustose corallines dominate mainly by default (i.e., under conditions of minimal competition), where corals are inhibited (e.g., by elevated nutrients or by strong wave action), and where fleshy algae are removed by intense herbivory. The wave-pounded intertidal algal ridges are built predominantly by *Porolithon* (*Hydrolithon*) *onkodes*, *P. gardineri*, *P. craspedium*, and *Lithophyllum kotschyannum* in the Indo-Pacific and *P. pachydermum*, and *L. congestum* in the Atlantic; all are coralline species that appear uniquely tolerant of aerial exposure. The transition from frondose- to turf- to coralline-algal communities has been reported (Steneck, 1989) to closely correlate with increasing herbivory gradients on coral reefs.

In addition to their protective reef-building nature, coralline algae provide a number of other goods and services. Since the eighteenth century, unattached corallines (maërl) have been harvested as acid-soil pH conditioners. In Britain and France, hundreds of thousands of tons of *Phymatolithon calcareum* and *Lithothamnion corallioides* continue to be dredged annually. Enormous maërl beds, several km<sup>2</sup> in area, mainly composed of species belonging to the genera *Lithothamnion* and *Lithophyllum*, are present off the coast of Brazil and have begun to be commercially harvested. Maërl is also used as a mineral food additive for cows, hogs, and other livestock, as well as in the filtration and neutralization of acidic drinking water. Corallines are used in modern medical science in the preparation of dental bone implants (Shors, 1999). The cellular carbonate skeleton provides an ideal matrix for the adherence and regeneration of bone and tooth structures. Coralline algal fossils have proven to be extremely beneficial in deriving paleoecological and paleoclimatic information, and also have been employed as stratigraphic markers of particular significance in petroleum geology. As a spectacularly colorful component of live rock for the flourishing marine aquarium trade, coralline algae are highly desired for their architectural and attractive aesthetic qualities. However, the most important contribution of coralline algae worldwide may well prove to be in ameliorating the greenhouse carbon dioxide buildup associated with global climate change. It is the balance between calcification and respiration – which produce carbon dioxide – and the consumption of CO<sub>2</sub> by photosynthesis that will determine whether corallines act as a “sink” (absorbing CO<sub>2</sub>) or as a source of CO<sub>2</sub>. Experiments that studied how various calcifying systems take up and give off carbon dioxide have shown that the rise in CO<sub>2</sub> produced by calcification is mitigated by its removal through increased photosynthesis (Ohde, 1995; Iglesias-Rodriguez et al., 2008), with a net effect that is unlikely to either contribute greatly or significantly reduce the rise in atmospheric CO<sub>2</sub>. However, rising levels of CO<sub>2</sub> and concomitant acidification of seawater inhibit all

reef builders, including coralline algae (Kleypas et al., 1999). By binding vast accumulations of CaCO<sub>3</sub> during calcification and photosynthesis, corallines may play a role in slowing future acidification of marine habitats such as coral reefs.

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## Cross-references

[Algal Rims](#)  
[Atoll Islands \(Motu\)](#)  
[Barrier Reef \(Ribbon Reef\)](#)  
[Calcite](#)  
[Coral Reef, Definition](#)

[Fossil Coralline Algae](#)  
[Fringing Reefs](#)  
[General Evolution of Carbonate Reefs](#)  
[Ocean Acidification, Effects on Calcification](#)  
[Pacific Coral Reefs: An Introduction](#)  
[Reef Front Wave Energy](#)  
[Reef Structure](#)  
[Rhodoliths](#)  
[Spurs and Grooves](#)

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## ALGAE-MACRO

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## Synonyms

Macroalgae; Macroscopic algae; Multicellular photosynthetic cryptogams; Seaweeds

## Definition

Macroalgae are multicellular marine plants that are easily observed by the unaided eye and whose “thallus” (plant body) is characterized by holdfasts for attachment, and by “laminae,” reproductive “sori,” gas bladders, and/or stipes. They lack the various structures that characterize higher plants, such as true leaves, roots, and encased reproductive organs.

## Introduction

Macroalgae (“seaweeds”) belong to either one of three groups of eukaryotic algae: the Rhodophyta (red algae), Chlorophyta (green algae), and Phaeophyceae (brown algae) or to the prokaryotic colony-forming Cyanobacteria/Cyanophyta (blue-green algae). These four groups do not have a common multicellular ancestor (i.e., collectively they are polyphyletic); although, their chloroplasts – common to all – appear to have had a single blue-green algal (Cyanobacteria) origin. The presence of chloroplasts and subsequent capacity for photosynthesis give marine macroalgae an ecological role as primary producer that is similar to other marine plants, notably “seagrasses.” However, seagrasses are not seaweeds; rather, they are rooted, flower, and seed-bearing “higher” plants (Angiosperms).

The macroalgal thallus (i.e., plant body) consists of blades (leaf-like lamina), reproductive sori (spore clusters), gas bladders [flotation organs (on blades in rockweeds, between lamina and stipes in kelps)], stipes [stem-like structures (may be absent)], and holdfasts [with or without haptera (finger-like extensions anchoring to substrates)]. The stipe and blade combined are known as the frond.

Macroalgae grow attached to stable substrata in seawater (or brackish water) under light levels sufficient for photosynthesis. Seaweeds are most commonly found in shallow waters on rocky shores; however, the green algal group Bryopsidales includes rhizoidal forms adapted



to proliferating in sedimentary environments. At the shallowest level are algae that inhabit the high-intertidal spray zone, whereas, the deepest living forms are attached to the seabed under nearly 295 m of water (Littler and Littler, 1994; see *Algae, Coralline*, Figure 10). The deepest macroalgae are calcified crustose coralline species.

### Human utilization of macroalgae

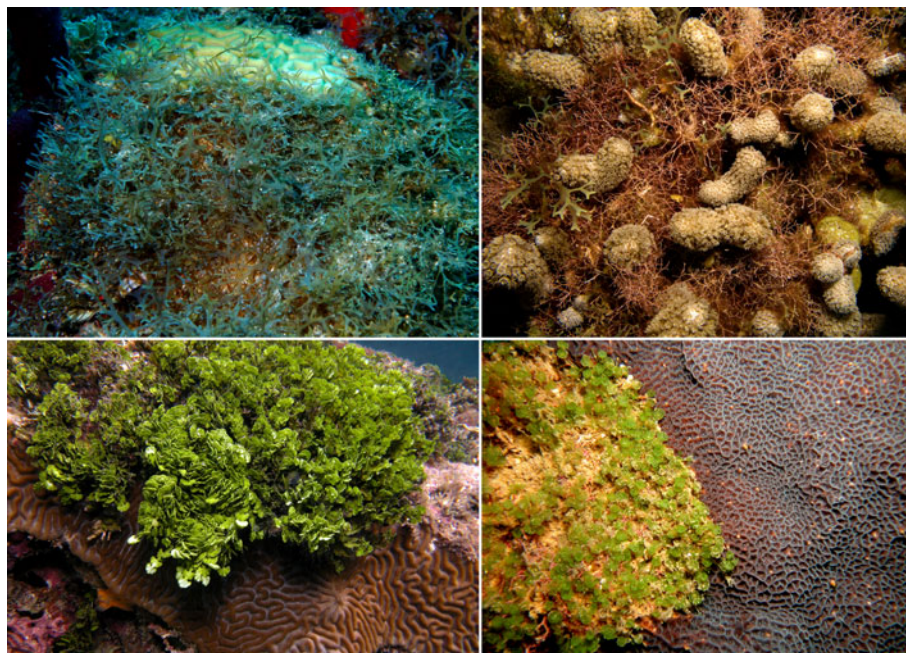
Macroalgae have a variety of uses. They are used extensively as food by coastal cultures, particularly in Southeast Asia. Seaweeds are harvested or cultivated for the extraction of alginate, agar, and carrageenan – gelatinous substances collectively known as hydrocolloids or phycocolloids. Colloids have great commercial importance, especially in the production of food additives. The gelling, water-retention, emulsifying, and other physical properties of colloids are critical to the food industry. Agar is used in foods such as candies, canned meats, desserts, bottled drinks, and gelatin molds. Carrageenan is used in the manufacture of salad dressings, condiments, dietary foods, as preservatives in canned meat and fish, milk products, and bakery goods. Alginates are utilized for many of the same uses as carrageenan, but are also used in the production of paper sizings, glues, colorings, gels, explosive stabilizers, fabric prints, hydro-spraying, and drill lubricants. Macroalgae have long been used as fertilizers and soil conditioners. Seaweeds are currently being investigated as sources of biodiesel and biomethane. Algal extracts are also widely used in tooth-pastes, cosmetics, and paints.

In the biomedical and pharmaceutical industries, alginates are used in wound dressings and production of dental molds. In microbiological/diagnostic research, agar

is extensively used as the culture substrate of choice. Seaweeds are also a source of iodine, an element necessary for thyroid function. The vast array of natural products that algae produce represents a potential “gold mine” of medicinal compounds that are still yielding promising results.

### Ecological significance of macroalgae

Top-down control of macroalgae by abundant populations of large mobile herbivores is particularly well studied for coral reefs, beginning over four decades ago with the caging study of Stephenson and Searles (1960). As examples, Sammarco et al. (1974), Ogden and Lobel (1978), Sammarco (1983), Carpenter (1986), Lewis (1986), Morrisson (1988), and numerous other workers (see review by McCook et al. (2001)) have demonstrated that lowering herbivory without increased nutrient inputs (usually assumed) mostly results in rapid increases in fleshy algae. However, when coral reefs are exposed to an increase in nutrients (bottom-up), fleshy macroalgae (Figure 1) may be favored over the slower growing but highly desirable corals (Lapointe et al., 1997). On healthy oligotrophic coral reefs, even very low nutrient increases may exceed critical levels that can shift relative dominances by stimulating macroalgal production, while inhibiting corals (Littler and Littler, 1984). Interestingly, large biomasses/standing stocks of slow-growing perennial macroalgae (e.g., rockweeds) can develop given sufficient time, even under low inorganic nutrient concentrations (McCook, 1999). Also, *Sargassum* spp. can coexist with corals in oligotrophic waters by utilizing particulate organic sources of nutrients (Schaffelke, 1999). Therefore, in this context, large macroalgal biomasses do not



Algae-Macro, Figure 1 Images of frondose macroalgae overgrowing corals.

necessarily require or indicate detrimentally abundant dissolved nutrients.

Fleshy macroalgae can outcompete corals (Birkeland, 1977; Bellwood et al., 2006), many of which are inhibited under elevated nutrient levels (reviewed in Marubini and Davies, 1996). Fast-growing macroalgae are opportunists that benefit from disturbances that release space resources from established longer-lived organisms. They can also take over space from living corals (Birkeland, 1977) when provided with sufficient nutrients. As a result, frondose macroalgae (those that form carpets of horizontal thalli) are generally recognized as harmful to coral reefs due to the linkage between excessive blooms and coastal eutrophication (ECOHAB, 1997). The competitive dominance of fast-growing macroalgae is inferred from their overshadowing canopy heights, as well as from inverse correlations in abundances between algae and other benthic producers (Lewis, 1986), particularly under elevated nutrient concentrations (e.g., Littler et al., 1993; Lapointe et al., 1997). Macroalgae, such as *Halimeda* spp. (Figure 2), also can gain competitive advantage by serving as carriers of coral diseases (Nugues et al., 2004). The fleshy macroalgal form-group has proven to be particularly attractive to herbivores (see Hay, 1981; Littler et al., 1983a, b) and only becomes abundant where grazing is lowered or swamped by excessive algal growth [chemically defended forms such as Cyanobacteria (Figure 3; Paul et al., 2007) are exceptions]. Overcompensation by high levels of herbivory may explain some of the reported cases (e.g., Smith et al., 2001) of specific corals surviving high-nutrient coral-reef environments.

### Major macroalgal groups

#### Rhodophyta (red algae)

Rhodophyta are generally some shade of red, the result of having large quantities of the red pigment phycoerythrin

in their photosynthetic cells. This red pigment in combination with various other pigments is responsible for the vast array of colors ranging from translucent pale pink, lavender, purple, maroon, burgundy to iridescent blue (Figure 4), but generally with some hint of red. The pigment phycoerythrin is water-soluble; therefore, red algae immersed in hot water will stain the liquid red or pink and the thalli will eventually turn green. Other red-algal characters are eukaryotic cells lacking motile gametes (without flagella and centrioles), floridean starch as the food reserve, and chloroplasts containing unstacked thylakoids without an external endoplasmic reticulum. Pit connections and pit plugs are unique and distinctive features of red algae that form during the process of cytokinesis following mitosis. Most red algae are also multicellular, macroscopic, marine, and have sexual reproduction. They display alternation of life-history phases including a gametophyte phase and two sporophyte phases.

The red algae are almost exclusively marine and comprise the most diversified and the largest group of tropical reef plants, with estimates of up to 10,000 species. Their diversity of forms is astonishing, ranging from small filamentous turfs to some of the larger and most beautifully delicate organisms on coral reefs (Figure 4). Calcareous red algae can dominate some reefs and often surpass corals in reef-building importance [e.g., *Porolithon* (*Hydrolithon*) *craspedium*, Figure 5]. Most often, corals (Cnidaria) supply the bulk building blocks, whereas, coralline algae do much of the cementing together of debris. The crustose coralline algae [forms that deposit a type of calcium carbonate (calcite limestone) that is harder and denser than the aragonite of corals] also build the “algal ridge” (see *Algae*, *Coralline*, Figure 5). The raised algal ridge, by absorbing tremendous wave energy, not only protects land masses that would otherwise erode, but also shelters the more delicate corals and other reef organisms.

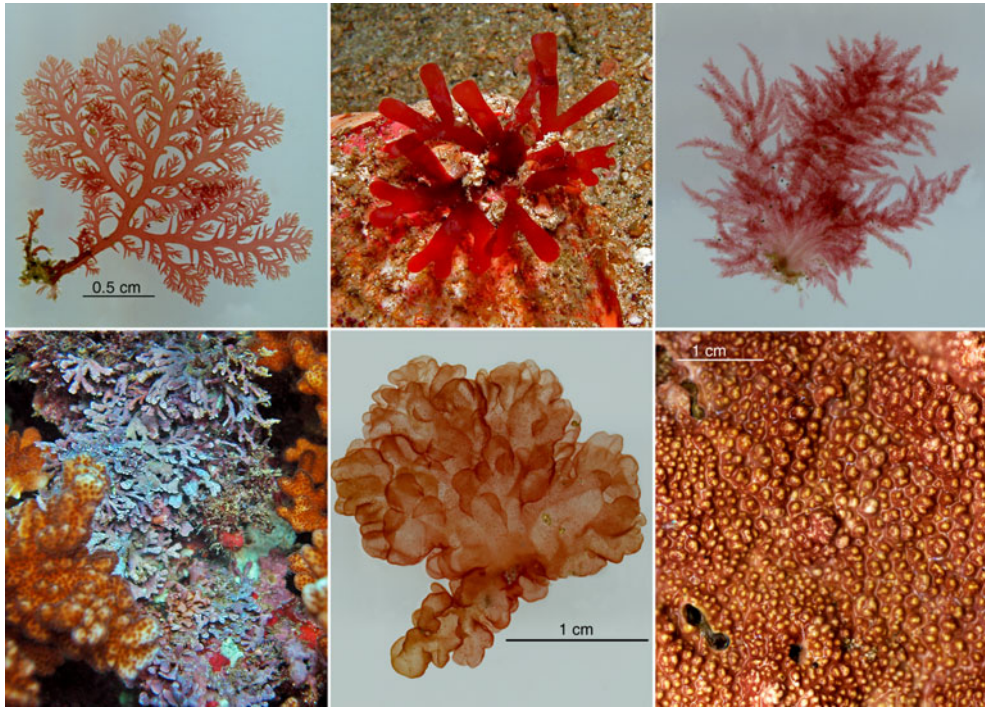


Algae-Macro, Figure 2 *Halimeda opuntia* competing with coral.



Algae-Macro, Figure 3 *Lyngbya polychroa*, a chemically defended blue-green alga overgrowing *Millepora*.





**Algae-Macro, Figure 4** Array of different forms and colors of red algae.

### Phaeophyceae (brown algae)

The most frequent color within Phaeophyceae is some shade of brown, from pale beige to yellow-brown to almost black. This color is the result of large quantities of the brown pigment fucoxanthin. Fucoxanthin is alcohol soluble and the liquid will turn brown after immersion of a specimen, with the thallus eventually becoming green. They have cellulose walls, with alginic acid and fucoidin also important components. Brown algae are unique among macroalgae in developing into multicellular forms with differentiated tissues, and they reproduce by means of motile flagellated spores. Most brown algae have a life history that consists of an alternation between morphologically similar haploid and diploid plants. *Scytosiphon lomentaria* alternates between four distinct morphological generations, which is considered to be a “bet-hedging” survival strategy (Littler and Littler, 1983).

The Phaeophyceae comprise about 2,000 species and are almost exclusively marine algae and, as kelps (Laminariales), attain their greatest abundance, size, and diversity in cold temperate to polar waters. They occur from the high intertidal (Fucales) to 115 m deep (*Sargassum hystrix*, Littler and Littler, 1994). Tropical brown algae include microscopic filaments, sheets, coarsely branched, and crust forms. Nearly all brown algae have fine (microscopic) hairs emanating from their surfaces that may serve to increase surface area for nutrient uptake.

Brown algae are also well represented and very important on coral-reef ecosystems, with certain species of rockweeds able to dominate the fleshy algal biomass in

back-reef areas. For example, *Sargassum* and *Turbinaria*, growing just behind the reef crest, can form small-scale forests up to several meters high that provide biomass, habitat, and shelter for numerous fishes and invertebrates. Interestingly, we have observed vast drifting rafts of floating *Sargassum* in Fiji that were reminiscent of the Atlantic Ocean’s Sargasso Sea accumulations.

### Chlorophyta (green algae)

The most representative color of the Chlorophyta is some shade of green, the result of having large quantities of predominantly green chlorophyll pigments. Chlorophyll is also present in all of the other algal divisions; however, members of those groups have additional pigments that often overshadow and mask the green chlorophyll color. The green algae, in addition to chlorophylls *a* and *b*, also contain various subordinate carotenoid and xanthophyll pigments. The green algae, with upwards of 7,000 species, are the ancestral relatives of vascular plants (grasses, trees, seagrasses, etc.), which also contain these same basic pigments. Green seaweeds range from microscopic thread-like filaments to thin sheets, while others are spongy, gelatinous papery, leathery, or brittle in texture, ranging to 1.5 m in length (Figure 6). The green algae store their energy reserves as starch; therefore, a drop of potassium iodide (tincture of iodine) on a branch or blade will stain blue-black (iodine is taken up by starch granules). All produce flagellated spores and gametes giving them the advantage of motility.



**Algae-Macro, Figure 5** The reef-building calcareous macrophyte *Porolithon* (*Hydrolithon*) *craspedium*.

Green algae are always present on tropical coral reefs and lagoon floors, often intermixed among seagrass shoots. These are the siphonaceous (giant-celled) forms of Bryopsidales, such as *Halimeda*, *Avrainvillea*, *Udotea*, and *Caulerpa* that employ a unique cytoplasmic streaming/blade abandonment mechanism to eliminate epiphytes (Littler and Littler, 1999). Most Bryopsidales have a rhizophytic “rooted” growth form and readily take-up pore water nutrients by cytoplasmic streaming (Williams, 1984). The deepest occurring fleshy upright alga (*Rhipiliopsis profunda*) is a member of this group and was found by submersible attached to bedrock at a depth of 210 m (Littler and Littler, 1994). Some genera of filamentous or sheet-like green algae are extremely tolerant of stressful conditions and can be indicators of fresh-water seeps, recently disturbed areas (as early colonizers of newly exposed substrates), habitats of low herbivory (high herbivory eliminates palatable greens), and especially areas with an overabundance of nutrients (e.g., bird roosting islands, polluted areas).

Calcified green algae are major contributors to the production of marine sediments. Some genera, such as *Udotea* and *Penicillus*, produce enormous amounts of fine silt and

other sediments due to continual sloughing and following disintegration. In many tropical locales, the sparkling white sand beaches are mostly bleached and eroded calcium-carbonate (aragonite) skeletons of *Halimeda*. “*Halimeda* hash” (i.e., the coarse oatmeal-like accumulations of *Halimeda* segments, Figure 7) has been used in power-generating plants and other fossil-fueled industries as smoke-stack scrubbers/neutralizers to precipitate sulfuric acid and other precursors to acid rain.

### Cyanobacteria (blue-green “algae”)

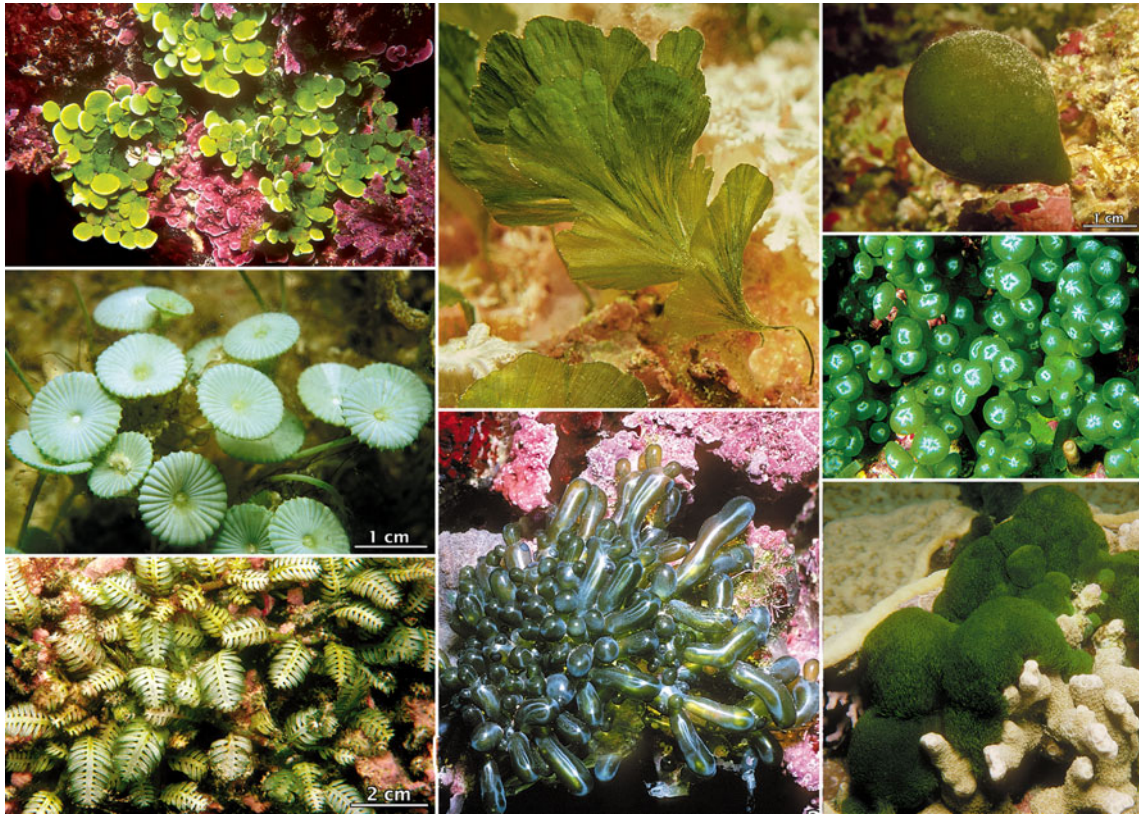
This ancient, highly controversial, and difficult group is a “prokaryote,” not a true plant. The Cyanobacteria were the first group to evolve photosynthesis, the process that powers the biological world. On tropical reefs, they comprise masses of microscopic organisms that are strung together into large filamentous clumps or colonies (Figure 8). In life, most of these large aggregations have distinctive colors, shapes, or growth forms that provide distinctive recognition features. However, these are lost in preserved specimens, and thus went unappreciated by earlier museum/herbarium-bound taxonomists. Most commonly, the color of blue-green algae is some peculiar shade of pink to purple to black – a combination of red from the pigment phycoerythrin, blue from phycocyanin, and green from chlorophyll.

Colonies may form filamentous tufts, sheets, or globular spheres (Figure 8). Some filamentous colonies show the ability to differentiate into several specialized cell types: vegetative cells (the normal, photosynthetic cells that are formed under favorable growing conditions), akinetes (the stress-resistant long-lived spores that form when environmental conditions become harsh), and thick-walled heterocysts, which contain the enzyme nitrogenase for nitrogen fixation (see below; Herrero and Flores, 2008). Heterocysts also form under specific environmental conditions (anoxia, hypoxia) or where nitrogen is limiting. Many Cyanobacteria also form motile reproductive filaments called hormogonia that glide free from the parent colony at special weaker cells (necridia) and disperse to form new colonies.

Like the other groups of seaweeds, excessive standing biomass of Cyanobacteria is usually considered detrimental to the health of coral-reef systems and people. They produce chemical compounds that can be toxic to fish, plankton, and invertebrates. For example, swimmers’ itch, a skin irritation that beach goers commonly experience, is caused by blooms of the blue-green alga *Lyngbya majuscula* (Figure 9). Black-band disease of corals (Figure 10), found throughout all tropical oceans, is caused by blue-green algae and associated microorganisms (Ruetzler et al., 1983). Certain Cyanobacteria produce neurotoxins, hepatotoxins, cytotoxins, and endotoxins that can be dangerous to animals and humans (Paul et al., 2007). Several cases of human- and many cases of livestock-poisoning have been documented.

The nitrogen fixing capacity of some blue-green algae is extremely important, although often overlooked.





**Algae-Macro, Figure 6** Array of different green algal forms.



**Algae-Macro, Figure 7** *Halimeda* "hash"; i.e., dead calcareous segments.

Heterocyst-forming species bind nitrogen gas into ammonia ( $\text{NH}_3$ ), nitrite ( $\text{NO}_2^-$ ), or nitrate ( $\text{NO}_3^-$ ) that can be absorbed by all plants. This role is crucial for tropical reef systems and especially nutrient-depauperate atoll reefs, which are extremely low in "fixed" nitrogen. Some of

these organisms contribute significantly to global ecology and the oxygen cycle. For example, the marine cyanobacterium *Prochlorococcus* (0.5–0.8- $\mu\text{m}$  diameter spheres) accounts for >50% of the total photosynthetic production of the open ocean and 20% of the planet's atmospheric oxygen (Partensky et al., 1999). Cyanobacteria are the only group of organisms that are able to reduce nitrogen and carbon in aerobic conditions, a feature that may be responsible for their evolutionary and ecological success.

Blue-green algae are abundant worldwide and ubiquitous on coral reefs, where they often occur under extreme environmental conditions. The universally present black band in the splash zones that make rocks or boat ramps slippery is a layer of microscopic blue-green algae. Such blue-greens can withstand exposure to severe drying, extreme salinity, rain water, bright sun, and high heat and still flourish. Cyanobacteria are the oldest known life forms on earth. Stromatolites containing fossilized oxygen-producing Cyanobacteria date to 1.5 billion years ago (Zhang and Golubic, 1987). The ability of Cyanobacteria to perform oxygenic photosynthesis is thought to have converted the early reducing atmosphere of Earth into an oxidizing one. Chloroplasts – the organelles responsible for photosynthesis in all higher plants and eukaryotic algae – evolved from Cyanobacteria via endosymbiosis.





**Algae-Macro, Figure 8** Array of different blue-green algal forms.

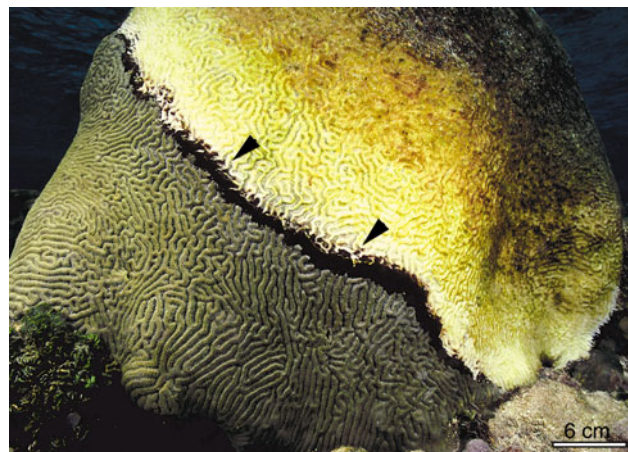


**Algae-Macro, Figure 9** Raft of the noxious blue-green alga, *Lyngbya majuscula*.

This evolutionary step dramatically changed the composition of life forms on Earth, triggering an explosion of biodiversity and leading to the near-extinction of oxygen-intolerant organisms.

### Summary

Marine macroalgae are among the oldest and most significant inhabitants of coral reefs. Because of the rapid degradation of tropical reefs worldwide, it is imperative that the role and diversity of macroalgae be studied in a timely,



**Algae-Macro, Figure 10** The black-band disease, *Phormidium corallyticum*, attacking a brain coral.

efficient, and scientifically verifiable manner. It is of paramount importance to characterize the world's coral-reef environments and to understand the responses of these foundation species. The fleshy macroalgal forms are the food of herbivores, and only become abundant when their rate of production exceeds the capacity of herbivores to consume them. On healthy oligotrophic coral reefs, even very low nutrient increases may shift relative dominance from corals to macroalgae by both stimulating macroalgal

production and inhibiting corals (Marubini and Davies, 1996). As a result, frondose macroalgae as a group are generally recognized as harmful to the longevity of coral reefs due to the linkage between excessive blooms and coastal eutrophication.

Reef plant complexity has evolved along very different evolutionary lines. The range of sizes, shapes, life histories, pigments, and biochemical and physiological pathways is remarkable. The biodiversity of coral-reef plant life is unequalled. Macroalgae from four evolutionary lines dominate and, in conjunction with coelenterate corals, are the major primary producers and builders of coral-reef habitats and carbonate architecture. Previously, marine plants have been understudied on coral reefs. However, their rapid growth and short generation time make them ideal subjects for experimental studies. Some are commercially valuable and/or preferred table fare for many humans. Marine plants are essential to the world's biogeochemical cycles and serve as potentially important sources of pharmaceuticals. The critical role that seaweeds play in reef ecosystems overlaps with other fields of marine sciences, such as fisheries resources, marine chemistry, ecology, geology, and coral-reef conservation.

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## Cross-references

[Algae, Blue-Green Boring](#)  
[Algae, Coralline](#)  
[Algae, Turf](#)  
[Algal Rims](#)  
[Fossil Coralline Algae](#)  
[Halimeda](#)  
[Halimeda Bioherms](#)  
[Nutrient Pollution/Eutrophication](#)  
[Rhodoliths](#)  
[Seagrasses](#)  
[Stromatolites](#)

## ALGAE, TURF

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### Synonyms

Algae turfs; Algal mats; Low-growing algae; Prostrate algae

### Definition

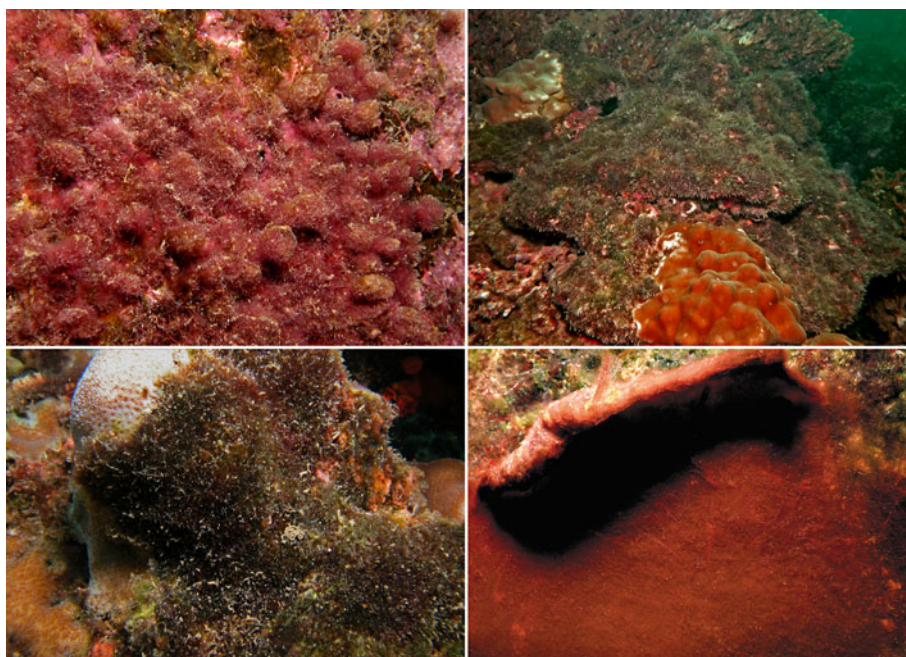
Algae turfs are sparse to thick mats of diminutive and juvenile algae less than 2 cm high.

Turf communities ([Figure 1](#)) are composed of juvenile macroalgae and faster-growing filamentous species

accompanied by the ubiquitous blue-greens, diatoms, and detrital sediments. These juvenile and microalgal species assemblages have a high diversity (>100 species in some western Atlantic turfs), although only 30–50 species commonly co-occur at any one time.

Turf algal assemblages, when viewed as a functional indicator group (Littler and Littler, 2007), remain relatively stable year round. They are often able to recover rapidly after being partially consumed by herbivores. Algal turfs characteristically trap ambient sediments and smother corals and other competitors for space by gradual encroachment. Domination by turf algae suggests not only desirably low nutrient levels (bottom-up) but also an inadequate herbivory (top-down) component required for healthy coral-dominated reefs (Littler et al., 2006). Algal turfs have been shown to form extensive horizontal mats under reduced nutrient-loading rates (Fong et al., 1987) or infrequent nutrient inputs (Fujita et al., 1988). Their relatively small size and rapid regeneration from basal remnants (perennation) results in only moderate losses to herbivory at low grazing pressures.

Turf algal community structure can be affected by the behavior of territorial damselfish. Because of their preferential grazing and protection (chasing off of larger herbivores), damselfish cultivate more diverse alga turfs that have higher biomass within their territories. Turf algae have opportunistic (“weedy”) life-history characteristics, including high surface area to volume ratios and the ability to maintain substantial nutrient uptake and growth rates



**Algae, Turf, Figure 1** Examples of naturally occurring algal turf communities. Upper left: *Asparagopsis taxiformis* Sporophyte. Upper right: *Gelidiopsis intricata*. Lower left: *Wurdemannia miniata*. Lower right: *Oscillatoria rosea*.



under low-nutrient conditions (Rosenberg and Ramus, 1984). Turfs also contain populations of nitrogen-fixing Cyanobacteria (Adey, 1998) that can enrich the other low-growing members within the dense turf community in oligotrophic waters.

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## Cross-references

Algae, Turf  
Nutrient Pollution/Eutrophication

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## ALGAL RIMS

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## Definition and morphology

Algal rims are marine biogenic formations of various size and shape, generally edificated by Coralline algae associated with other organisms, developing upon the windward edge of coral reefs or rocky coasts in tropical and subtropical seas.

Thin reef-like structures (often referred to as biostromes) may develop on the outer edge of reef-flats or rocky windward coasts submitted to strong surf, both in tideless or tidal areas. They were first described from the Pacific (Tracey et al., 1948), and were subsequently found in the North Atlantic (Agassiz, 1895), Brazil (Kempf and Laborel, 1968) and the Caribbean area (Gessner, 1970; Adey and Burke, 1976). Related formations are also known from the Mediterranean (Blanc and Molinier, 1955). They are mainly built by massive or encrusting coralline algae (mostly *Hydrolithon*) Hydrocorals (*Millepora* spp.), Vermetid Gastropods and some corals. Specific

composition varies with surf, slope and nature of substrate (Focke and Gebelein, 1978). Plant and animal populations mingle seaward with those of the reef's outer slope; laterally, the rim may pass to the spur-and-groove structures or to rim-like formations developing directly on rocky shores.

On coral reefs, algal rims often develop by fusion of algal heads. Extreme surf conditions may lead to the development of boilers, terraced pinnacles or blowholes.

Similar morphological structures may be obtained by erosive processes. Bermudian "erosive boilers" generated from the erosion of an emerged stack of soft rock were described (Ginsburg and Schroeder, 1973).

## Relation with sea level

- Some biological components of algal rims (*Dendropoma* vermetids, some *Lithophyllum* and *Hydrolithon*) have a very narrow repartition around MSL; their presence in cores or on elevated shorelines is a precise indicator of past sea levels, with metric or decimetric approximation, and widely used around the world's oceans (Adey, 1986; Pirazzoli et al., 1988; Laborel et al., 1994). Stony corals having a range of – 5 to 10 m tend to be less accurate indicators.

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### Cross-references

Algae, Coralline  
Forereef/Reef Front  
Reef Front Wave Energy  
Spurs and Grooves

## ANTECEDENT PLATFORMS

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### Definition

Antecedent Platforms are the surfaces, usually older reefs which have been exposed to the atmosphere, and which form the foundation for later reef growth.

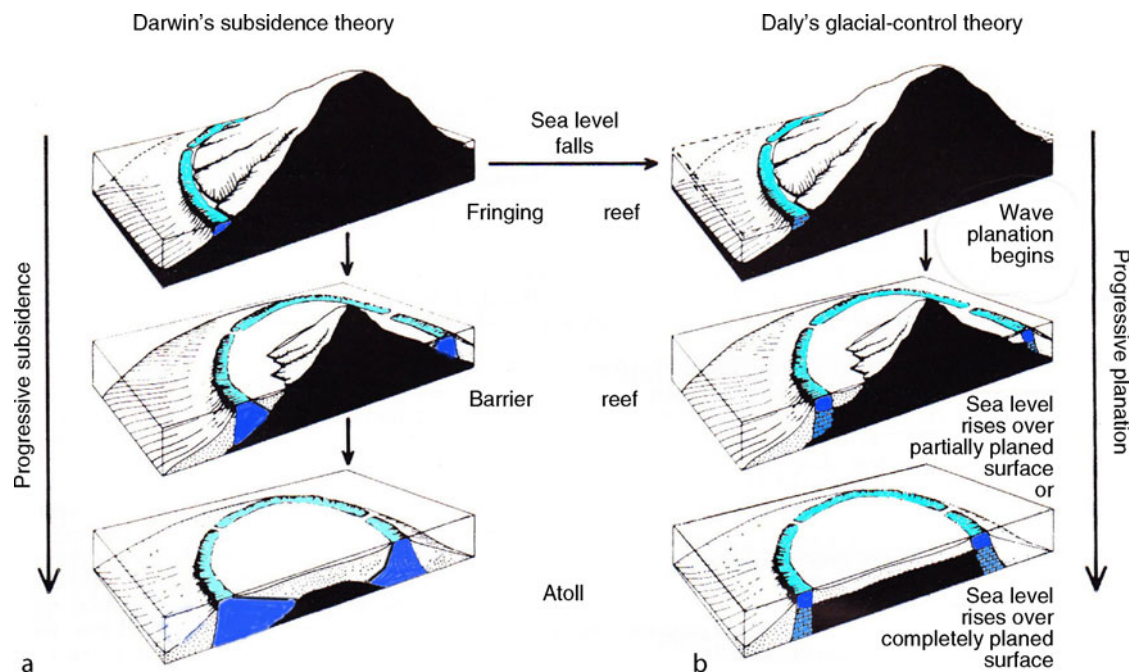
### Introduction

In the study of coral reefs, the term “antecedent platform” has a special place for three reasons. First, in various guises, it stood as a challenge to Darwin’s championing of subsidence as the principle factor in coral reef growth; second,

it stood against the need for glacial eustasy as a factor in reef growth; and third, as a special case (limestone platforms), and at a later time, it co-defined a new paradigm for the evolution of the foundations of modern reefs. The thinking on antecedent platforms moved therefore from the broad to the specific, from “the alternative” to “center-stage,” albeit coupled with other processes. This contribution traces these views accenting more the later process-related views but placed within the context of the earlier history.

### In the beginning!!

In the middle and early nineteenth century, ideas on reef evolution and growth were dominated by Darwin’s theory that subsidence played a critical role in the evolution of coral reefs from fringing to barrier to atolls (1842) (Figure 1). However, not all agreed on either the occurrence or primacy of subsidence in reef growth. A succession of contributors proposed that reefs accumulated on pre-existing reef platforms (Rein, 1870, 1881), volcanic foundations in the deep sea (Murray, 1880, 1887, 1889), or surfaces of submarine planation (Wharton, 1890, 1897; Gardiner, 1898, 1903, 1904; Agassiz, 1898, 1899). Indeed, Andrews (1900, 1902), for example, proposed that the Great Barrier Reef itself rested on a surface of submarine planation. All attempted to counter the need for subsidence in the evolution of coral reefs, and this continued even after the results of the Funafuti borehole were published, which showed that subsidence at any rate was a crucial factor operating in the evolution of at least that reef (Cullis, 1904), and



**Antecedent Platforms, Figure 1** (a) The Darwinian evolution of coral reefs and (b) Daly's glacial control theory of reef evolution. (Page 10 – Purdy'd 1974 paper.)

subsequent drilling throughout the Pacific has confirmed this (Schlanger, 1963). However, post-Funafuti, the importance of the antecedent platform was as a foil to another idea in understanding the growth of coral reefs, that is, glacial eustasy. In a series of controversial papers, Daly (1910, 1915, 1917, 1919, 1934) proposed that global glaciations had the effect of both lowering sea level and reducing sea surface temperatures, the effects of both substantially impacting the growth of coral reefs. His glacial-control theory, applied initially to atolls, used the glacial lowering of sea level to produce foundations, which were then planated by wave abrasion as the effective process in turning fringing reefs into barrier reefs and then into atolls (Figure 1b). These ideas were extended by Daly himself and by Vaughan (1914, 1919, 1923) to Florida and the Bahamas as well as to the Great Barrier Reef. While some of Daly's evidence has been called into question (e.g., not all atolls have the same depth; his proposed processes and rates of processes are unrealistic, and his proposed time-scales are wrong), there can be little doubt today that glacio-eustatic sea-level fluctuations have profoundly affected how we think about the nature of the platforms on which today's coral reefs have grown. The next step was taken by Kuenen (1933, 1947) coupling glacially produced sea-level fluctuations and subsidence to sub-aerial and marine intertidal erosion to produce partially or completely planated antecedent platforms on which further reef development could occur. And then, in the 1940s, very important papers but in poorly distributed publications, Japanese scientists (Yabe, 1942; Asano, 1942; Tayama, 1952) coupled glacio-eustatic sea-level fall to the nature of the reef foundations for the first time. Thus began the germ of a new set of ideas. The first two papers were by Hoffmeister and Ladd (1944, 1945), which admitted to the reality of sea-level fall but placed the major emphasis on a suitable substrate for subsequent reef growth, that is, any bench or bank situated at a proper depth in the coral seas is a potential reef foundation. In the 1945 paper, however, they reported the results of experiments simulating the effects of rainfall on an exposed limestone surface (a slab of Solenhoffen limestone) as a way to explain the origin of raised atolls. They inferred from their crude experiments that the saucer shape of raised atolls may be related to solution. This was left to MacNeil (1954) who accepted Kuenen's coupling of glacial lowering of sea level and subsidence but invoked sub-aerial erosion to produce the diagnostic annular rim of atolls, which was therefore inherited from a period of earlier sub-aerial erosion (Figure 2). The saucer-shaped basin was therefore the logical consequence of sub-aerial solution acting on exposed Pleistocene atoll foundations.

MacNeil (op.cit) emphasizes the importance of limestone-solution processes involving surface and sub-surface solution and re-deposition and surface case hardening in producing relief features inherited by subsequent reef growth during an ensuing sea-level rise. The accent was clearly placed on inheritance from an exposed eroded surface. Thus, atoll lagoons form on eroded lows, and atoll

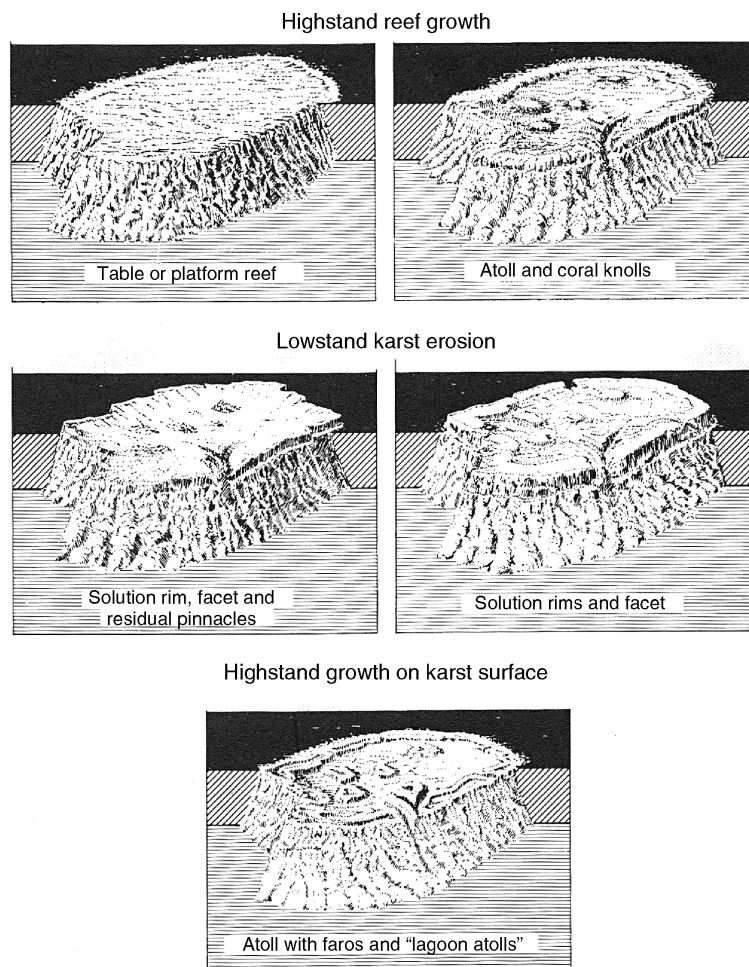
rims occupy the surrounding highs. For whatever reasons, MacNeil's ideas were not received with ultra-enthusiasm by the scientific community.

### Antecedence post-1974 – the purdy revolution

In 1974, Purdy (1974) published a seminal paper, inferring cause and effect in linking reef shape to karst-induced antecedent morphology. Drowned atolls reflect drowned karst topography; reef passes originate as drainage breaches in the solution rim; faroes are the karst product of breaching; peripheral islands are exposures of the fossil drainage divide, and spurs and grooves are expressions of lapies. Thus, the karst-induced differences in relief are perpetuated and indeed accelerated by growth, but reef growth per se has little to do with the basic configuration. Paradoxically, a paper proving that the Holocene reef off the north Jamaica coast was a mere mantling of low sea-level Pleistocene terraces (Goreau and Land, 1974) was published alongside Purdy's karst revolutionary paper.

In marked contrast to MacNeil's ideas, the 1974 paper sparked a widespread rethink of the role of antecedence and for a number of reasons: (1) Purdy's ideas applied to barrier reefs as well as atolls and therefore to a much wider scientific community, (2) he discussed processes that were important to the oil industry in developing porosity, once again opening the subject to a science community outside of the academic, (3) he coupled eloquent laboratory experiments to well-illustrated examples of mega-karst morphology from some of the world's notable karst areas, and (4) he used well-illustrated seismic data coupled to drill-hole data across a major barrier reef complex (effectively for the first time), which became well known through the work of Ginsburg and coworkers (Ginsburg and James, 1976; James and Ginsburg, 1976) and Rutzler and Macintyre (1982). Furthermore, when data was lacking he resorted to compellingly acceptable eloquent deductions. Like Hoffmeister and Ladd (1944), Purdy (1974) subjected limestone blocks to acid rain and produced features analogous to both karst and modern reef forms (Figure 2). He emphasized solution rims, enclosed depressions at various scales, conical karst, tower karst, and karst marginal plains as important natural and experimental features, which could have analogs in both atolls and barrier reef systems. He coupled glacially effected sea-level oscillations, subsidence, and sub-aerial erosion to explain their formation (Figure 3). Atoll morphology derives from the development of solution rims on emerged limestone masses; where rainfall is high, breaches in the karst rim give rise to subsequent atoll-passes, while in the interior, a conical karst may develop as antecedent foundations to lagoonal patch reefs; also, collapse dolines may form as a consequence of extensive subterranean dissolution, the forerunner of "blue holes" according to Purdy (1974). Alternately, where rainfall is low, conical depressions (solution dolines) form within the solution rim. The morphology of atolls and barrier reefs is solution determined rather than growth predicated (Purdy and Winterer, 2001) (Figure 4).



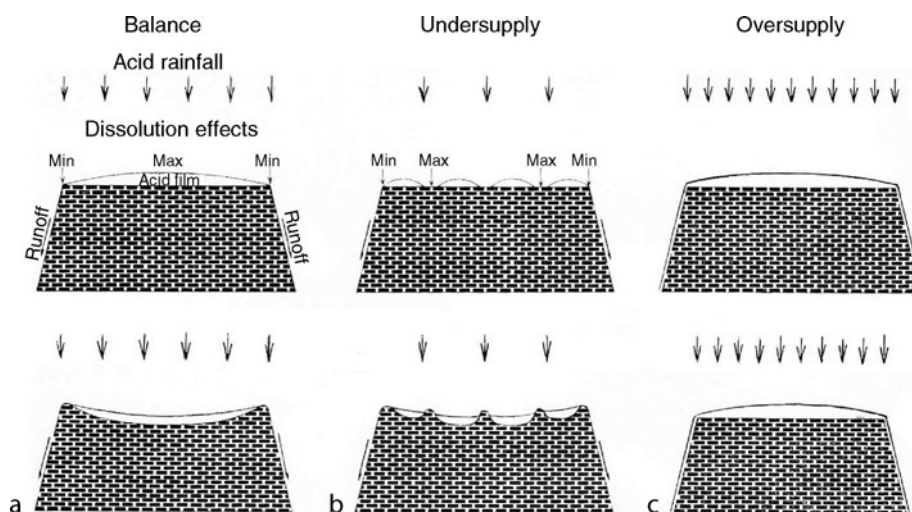


**Antecedent Platforms, Figure 2** MacNeil's (1954) diagram showing the development of atolls and faroes from sub-aerial erosion forms. (See Hopley (1982, p. 19).)

General support for Purdy's ideas comes from the saucer shapes of many modern reefs, the many enclosed depressions within them and the fact that many modern reefs are underlain by earlier reefs. In addition, there can be little doubt that some tropical karst landforms do have similar morphologies, as evidenced particularly in the atolls at Kita Daito Jima, at Mare and Lifou in the Loyalty Isles, and at Makatea in the Tuamotus (Bourouilh 1977). More recently, Purdy and Winterer (2001) show convincingly that atoll-lagoon depths (and therefore gross atoll morphology) are directly related to the amount of rainfall and the catchment size, indicating solution as a dominant process, but one which occurs accumulatively over many solution periods. In spite of this wealth of support however, it is Purdy's description and deductions regarding the evolution of the Belize Barrier Reef (Purdy, 1974) that add major weight to his hypothesis. Of particular importance are the identification of joint-related dolines in the northern region, the development of onshore karst dipping eastwards below the present shelf, the relations of the central province rhomboid shoals to underlying pre-Holocene

morphologies, and, most importantly, the southward narrowing of the Belize Barrier along a proposed karst-marginal plain increasingly effected by the proximity of the silica-dominated Maya mountains and increased rainfall. Underlying this detail, Purdy et al. (2003) also document an essential structural control on the distribution of platforms on which the carbonates have been disposed. In short, Purdy and his coworkers have covered the field in elucidating the geological and climatologic factors that have combined to produce the Belize Barrier Reef system, but emphasizing the importance of low stand sub-aerial erosion in sculpting the gross architecture.

In spite of the above, however, not all have been convinced of the role of karstic antecedence. From a theoretical viewpoint, young reef limestones are not thought to be mechanically suited for karst development (Jennings, 1971) while Ollier (1975) demonstrated conclusively that in a high rainfall region like the Trobriand archipelago off New Guinea, the raised Quaternary reefs have undergone very little surface karst erosion. Further, on the exposed raised reefs of Barbados, the extent of karstic



**Antecedent Platforms, Figure 3** The effects of rainfall on blocks simulated by dripping acid onto limestone surfaces (a) Rainfall (acid) is sufficient to produce a single acid meniscus over limestone surface; this produces a peripheral rim; (b) Rainfall (acid) insufficient to cover top surface so meniscus breaks up into a series of smaller menisci; the result is a rim bounded block in which the central depression has been residual solution prominences; and (c) Rainfall (acid) is more than sufficient and runs down the blocks: result is that the block just gets smaller.

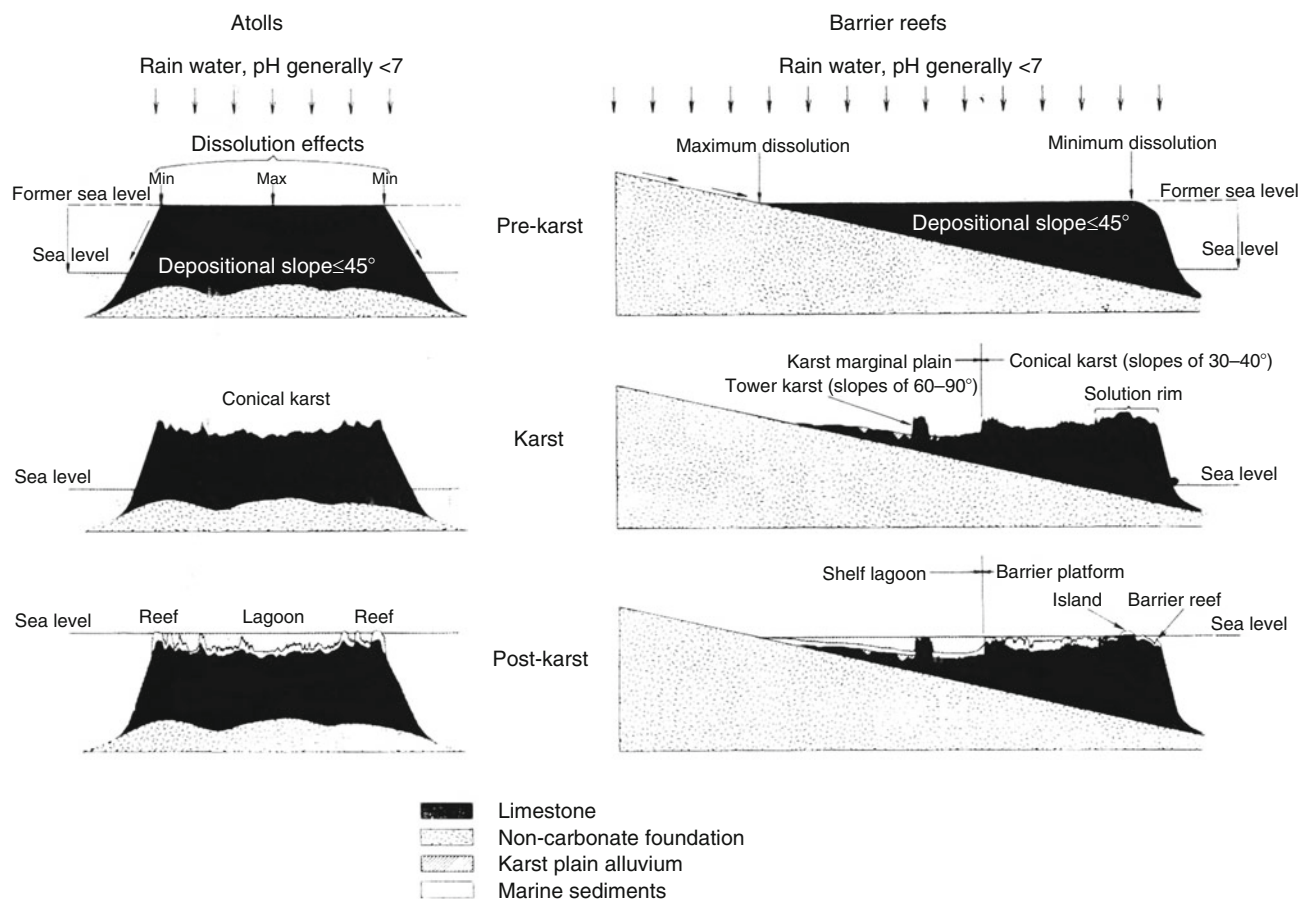
solution is directly related to the age of the limestones, that is, depressions in the 120 k reef are only 1 m deep, while in the >480 k reef, they are 12 m deep. Clearly, any karstic solution is cumulative, and Purdy (1974) recognized this, repeating again in 2001 (Purdy and Winterer) that in terms of gross morphology, the dissolution process is cumulative. Most now agree on this. However, an important question is still the extent to which the previous reef (usually the 125,000 years old reef) has affected the growth pattern of the modern reef, and this will depend on the amount and degree of erosion of the previous reef. Purdy himself was unsure about this, noting the work by Land et al. (1967) again on Bermuda and concluding that a net reduction of the exposed surface by up to about 4.5 m was likely. However, as a general conclusion, this is at odds with the facts, that is, beneath Belize and the Great Barrier Reef, the depth to the 125 k antecedent surface can be anything from –10 to –25 m below present sea level. Assuming the 125 k reef grew to sea level, then the present depth indicates 10–25 m of erosion plus subsidence in the intervening period, clearly at odds with the Bermuda conclusions. It is however in agreement with conclusions in Purdy and Winterer (2001) for gross surface erosion rates on Pacific atolls. In addition, if one uses the vertical erosion rates for coral and coralline algae published by Trudgill (1976) for Aldabra, then vertical erosion of the coral flat and algal flats in the Great Barrier Reef and exposure for around 95,000 years out of the last 125,000 years, then the surface of the 129 k reef is eroded only about 10 m. Coupled with estimated subsidence in the same time frame (5 m or so), the pre-Holocene surface would be at –10 m prior to the growth of the Holocene reef. This is in fact the depth that it is at on a number of reefs in the Great Barrier Reef (Davies and Hopley, 1983). While this solution/erosion is enough

to produce small-scale features, some of which may be inherited by the modern reef, it is clearly insufficient to have produced the large-scale features on the scale of barrier reef systems or reef tracts. Such features, Purdy says are the result of repetitive cumulative karstification. In the Great Barrier Reef, the idea of a karst marginal plain is no longer in favor (Hopley et al., 2007).

Since the seminal 1974 paper, Purdy has become more sure of his ground although even in 1974, he showed the direction in which his thoughts were moving – “Thus the major premise of the subsidence theory (Darwin’s) has been confirmed. It would be dangerous, however, to assume that this subsidence necessarily proves the genetic succession of reef types advocated by Darwin” (Purdy, 1974, p. 10). Further, quoting Vaughan’s warning in 1919 (p. 325) – “although the theoretical possibility of the conversion of a fringing reef into a barrier reef and a barrier reef into an atoll may not be denied, no instance of such a conversion has yet been discovered,” Purdy makes it clear that the evolution of reef types proposed by Darwin is open to question. In 2006, he states that “there are no examples of the subsidence-predicted transition of fringing reefs to barrier reefs to atolls. Moreover, the common occurrence of fringing reefs within barrier reefs negates subsidence as a causal factor in their presumed progressive evolutionary development” (Purdy and Winterer, 2006, p. 143). Instead, Purdy advocates a solution morphology template accentuated by reef construction particularly for barrier reefs.

### Growth antecedence

This was first proposed by Bloom (1974) and states quite simply that original reef facies exerts a fundamental control



**Antecedent Platforms, Figure 4** Diagrammatic evolution of atolls and barrier reefs according to antecedent karst theory. (Purdy Page 71)

on antecedence inheritance. The highly permeable reef framework and coarse rubble facies would be more resistant to solution erosion as they would be the highest above the water table and rainwater would pass rapidly through. Uncemented lagoonal sand and mud facies however would more likely be susceptible to solution. Thus, weathering across the reef would emphasize the constructional relief differences between reef and lagoon floor, such that re-submergence would situate reef facies above reef facies and lagoon facies above lagoon facies. This is not at odds with Purdy's ideas (above) as was proposed by some, but is a special case of it, as the karst is occurring on reef limestones (whereas Purdy's experiments and actual examples showed karst developing on most limestones).

Proof for these ideas requires detailed analysis of lithology immediately above and below the unconformity separating two periods of reef growth, and has been shown particularly in Belize but also in the reefs of the southern Great Barrier Reef where detailed mapping of facies distribution has occurred. At Ambergris Cay, at the northern end of the Belize Barrier Reef, Tebbutt (1975) showed that the exposed Pleistocene facies is a reef crest limestone with the same assemblage of corals as the modern reef crest.

A priori, however this shows reef growing on reef. In the southern Great Barrier Reef, a similar relation occurs. In particular, the algal rim some 50–100 m wide, which acts to protect the reef from wave destruction during the high stand, also offers protection during the low stand against sub-aerial weathering. It is dense, hard, and has a much reduced porosity compared with the adjacent open framework coral dominated facies in front and behind. The reef flat coral facies (leewards of the algal flat) which is 200–300 m wide, has a high porosity with a likely low retention time for percolating water during sub-aerial conditions. The sand flat facies between the coral flat and the lagoon has 40% porosity and is unlithified; it forms a boundary of around  $30^\circ$  with the lagoon and would be subject to substantial erosion and re-deposition down slope during periods of emergence. This unlithified edge would therefore retrograde backwards towards the inner edge of the coral flat. The reef front facies, in spite of being well lithified is also highly porous, and would be prone to cavern development and collapse under the influence of gravitational instability. Erosion would therefore be greatest in two areas, the fore reef (front, spurs, and grooves) and also along the edge of lagoon and sand flat. The effect of these specific areas of



erosion would be that the algal-dominated reef flat and the coral flat will stand up as a high rim. During the ensuing submergence, a new reef will first occupy the high ground on the previous reef and eventually grow at a still stand sea level with bio and sediment facies distribution similarly distributed to the reef below. Note that some modern patch reefs grow on top of earlier patch reefs, indicating a quite specific control on re-growth; that is, the reef is not growing on conical karst but on earlier patch reefs. Thus, in the Pleistocene, dominated by oscillating sea levels, a stacked succession of reefs will form through the combined effects of sea-level change, subsidence, and sub-aerial erosion (see Davies et al., 1988). In the case of the southern Great Barrier Reef, the periods of reef growth have been short (<10,000 years) compared with the periods of sub-aerial erosion of the previous reef (around 100,000 years). The driving force for the amount of reef stacking is clearly the frequency and magnitude of sea-level change.

The likelihood that this model also applies to Pacific atolls is high because they have a similar shape and facies distribution to that described above for the reefs of the southern Great Barrier Reef. The effects of a sea-level fall on an atoll would be to particularly expose the highly porous reef front, much of which would be removed and re-deposited down slope. The algal flat however would resist rapid erosion and form a protective cap above the catch-up coral facies below. The lagoon would remain a depositional low, although depending on the magnitude of the sea-level fall, it may contain a low stand lake or a saline pool connected to the ocean through the body of the exposed reef. Subsequent reef growth would eventually stack above the previous reef. Expansion of the facies laterally would be impossible on the outside of the reef because of the steep slopes. An example of such growth is Mururoa (Buigues, 1985; Guilcher, 1988), in that most atolls have similar characteristics to Mururoa (reef top biofacies distribution and steep external slopes inhibiting facies migration on the front), and most would also react to sea-level oscillations in the same way. Thus, in the Pleistocene at any rate, the high stand growth of platform reefs and oceanic atolls reflect two factors: (1) a high stand facies control of low stand produced inheritance features and (2) growth controlled largely by the direction and amount of energy input (See *Great Barrier Reef: Origin, Evolution, and Modern Development*; also Davies, 1983; Davies and Hopley, 1983). It is important to note however that in this model rapid sea-level oscillations are important. Change the oscillation pattern and a different effect will occur. For example, increasing the length of the low stand period may obliterate the effects of facies control. Increasing the lengths of the high stand will serve only to produce flat topped reefs.

### Non-karst antecedence

Reef growth has been shown to occur on antecedent surfaces that are not limestones. In the Pacific, Murray's original ideas (1880, 1887, 1889) that volcanics form a surface off which reefs have grown holds true. Perhaps less

obvious, however, are Choi and Holmes (1982) and Choi and Ginsburg (1982) work that show that late Pleistocene and Holocene reefs are growing on siliciclastic sediments, which have an alluvial and delta-like morphology. The residual relief of these coastal plain sediments localized initial coral growth; favored sites for such growth were elevations such as levees and bars of remnant channels and deltaic lobes. Thus, the unique rhomboid and long sinuous lagoon reefs are derived from the early Pleistocene river morphology and not from a fault dominated karst morphology as suggested by Purdy (1974).

### Conclusions

A consideration of reefal platforms began with Darwin's startling hypothesis that subsidence was paramount and drove fringing reefs to become barrier Reefs and ultimately atolls. In opposition the role of substrate was raised early, and then in conjunction with glacial control and sub-aerial erosion, it has risen to a position of general acceptance as a dominating process in the evolution of barrier reefs and atolls. Such antecedence is generally limestone based, and in some cases that antecedence has been shown to be facies controlled. However, antecedence has also been shown to occur off siliclastic foundations. There can be little doubt, however, that much antecedence is produced by low sea-level erosion.

Atolls are underlain by subsiding volcanic basements with steep peripheral slopes and surrounded by deep water. The limestones comprising the atoll platform can be tropical or temperate depending on their latitudinal position. During periods of oscillating sea level, the platform surface may be exposed, and karstic erosion set in, the effects of which will be the development of a raised rim which may or may not be breached, a central depression and conical karst features within the lagoon. Subsequent sea-level rise will allow growth preferentially such that it mimics the positive underlying topography, thus inheriting the eroded shapes.

In the formation of Barrier Reefs, a critical feature is the formation of a "karst marginal plain" – effectively an exposed shelf, carbonate dominated in the outer part and siliceous or non-carbonate in the inner part (effectively most shelves) – exposed as a consequence of a fall in sea level. Consequent sub-aerial erosion would occur to a maximum at the boundary of carbonate/non-carbonate rocks effecting the formation of tower-karst. Elsewhere in the carbonate-dominated area, a raised rim would form proximal to the outer steep slope (a la atolls) and conical-karst would form over the outer carbonate shelf (Figure 2). Following the subsequent rise in sea level, platform reefs would develop over the tower-karst and a barrier reef would develop over the outer shelf rim.

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## Cross-references

[Accommodation Space](#)  
[Belize Barrier and Atoll Reefs](#)  
[Bermuda](#)  
[Great Barrier Reef Committee](#)  
[Sea Level Change and Its Effect on Reef Growth](#)  
[Subsidence Hypothesis of Reef Development](#)

## ARAGONITE

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### Definition

Aragonite is a mineral comprising calcium carbonate ( $\text{CaCO}_3$ ), it is polymorphous to *calcite*, meaning that they both contain the same main elements but have different crystal structures. Aragonite forms orthorhombic crystals, whereas *calcite* is trigonal. Aragonite is characterized not only by pseudo-hexagonal crystals but also acicular habits, often in the form of radiating groups of needles, which are also common. Aragonite has an imperfect to poor cleavage, a subconchoidal fracture, and a hardness on Moh's scale of 3.5–4. Aragonite tends to be colorless or white, and most are relatively pure, with strontium and lead, acting as the most common substitutions for calcium. Aragonite is highly soluble in cold dilute hydrochloric acid, resulting in significant effervescence. Feigl's solution stains aragonite black, whereas *calcite* remains unaffected.

Aragonite most commonly precipitates in seawater and so is found in marine sediments and forms the shells of some marine organisms. The skeleton of scleractinian corals are composite organo-minerals comprising organic matrices and inorganic aragonite crystallites. Aragonite is a meta-stable form of calcium carbonate and over time undergoes transformation to the more stable *calcite* polymorph. Aragonite is more soluble than *calcite* in the meteoric environment and dissolution results in the partial or total loss of the aragonite clasts, matrix and cements, often leaving molds. These molds along with primary pores may subsequently be infilled by allochthonous *calcite* cement.

Alternatively, neomorphism may occur by a concomitant dissolution of aragonite and reprecipitation of autochthonous low-magnesian *calcite* cement (e.g., Rabier et al., 2008). On land, aragonite can be found in dryland environments associated with evaporite minerals such as halite and gypsum. Aragonite also forms speleothems in caves, tufa, and travertine as well as sinter in hot springs.

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## Cross-references

[Calcite](#)

## ATOLL ISLANDS (MOTU)

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### Synonyms

Cays; Gravel islands; Islets; Keys; Rubble islands; Shingle islands

### Definition

Atoll islands are morphologically coherent wave-built accumulations of bioclastic sediment, located on atoll rims or on patch reefs within atoll lagoons, and emergent at all stages of the tide. They can be of any size and shape and are characterized by low elevation (typically 2–4 m above MSL), shallow alkaline soils, absence of surface water, and a limited terrestrial biota. Atoll islands are composed of skeletal sands and/or coral rubble sourced from the adjacent reef or lagoon. On sea-level atolls, islands are geologically very young having accumulated during the mid-late Holocene. In spite of this short time frame, some unconsolidated island sediments have become indurated to form phosphate rock, cay sandstone, beach rock, and beach conglomerate, which offer some stability to atoll islands. *Motu* (n) is the word for any island or islet in many Polynesian languages, including Maori, Tuvaluan, and Paumotu, although the word has been given more specific meanings in coral reef geomorphology.

### Number, dimensions, and location of atoll islands

*Atolls* are annular reefs around a central lagoon. The reef rim may be continuous, or broken by a few channels as is common in the central Pacific, or have many shallow passes or *hoa* as in French Polynesia, or deep passages as in the *Maldives*. Rarely are rim reefs completely



occupied by islands, and equally rarely are no islands present. In the Maldives there are about 1,200 islands in its 21 administrative atolls, while in the Tuamotus most of the 75 atolls have over 20 islets each, with about 280 islets on the atoll of Raroia. Wiens (1962) has shown that the number of islands on atolls and the area they occupy decrease westward across the Pacific from the Tuamotu archipelago to the Caroline Islands.

Atoll islands are small and often cover only a small fraction of the available reef space. For instance, on the five main atolls in Tuvalu (Nanumea, Nui, Nukufetau, Funafuti, and Nukulaelae), there are 113 islands that occupy just 1–18% of the possible reef platforms. Here the average island size is 13 ha, but the majority are tiny with fifty-one <1 ha, another twenty-seven <5 ha, and only four >100 ha, the largest being 220 ha. Similarly, in the Maldives on South Malhosmadulu atoll there are 53 islands with a mean size of 10 ha and range from <1 to 46 ha. On this atoll the average proportion of reef platform occupied by islands is 28%, with a range from <1 to 71%. In both Tuvalu and the Maldives frequency distributions of island size and proportion of available reef occupied by islands are strongly skewed toward the lower values, a common situation throughout the atoll world.

Within atolls, islands are unevenly distributed around the reef rim to windward and leeward, particularly in the Pacific where the trade winds dominate. In many cases islands are concentrated along the eastern (windward) reef, with a tendency toward the southeast sector in the Marshall Islands and the northeast in the Tuamotus. Frequently, these windward islands are narrow linear features which tend to be closer to the lagoon shore than to the ocean reef edge. Along the western side (leeward) of Pacific atolls the reef is often discontinuous with fewer and more compact islands. Islands are rare within lagoons of Pacific atolls. In the Indian Ocean the distribution of reefs and islands is different. In the Laccadive–Maldivian archipelago, atoll rims are typically more open, and islands occupy reefs both around the eastern and western margins as well as within the central lagoons. This more regular distribution of islands is primarily a consequence of the seasonal reversal in monsoonal conditions.

## Motu

In coral reef literature, the Polynesian word *motu* has a more restricted meaning than simply “island” or “islet,” although usage has not been consistent. In Stoddart and Steers’ (1977) classification, reef islands with a high seaward shingle ridge or ridges and a lower sand area to leeward are called *motu*, to distinguish them from pure sand cays or pure shingle cays. Such *motu* are typically associated with high-energy environments on the windward rim of atolls. Other authors equate *motu* exclusively with coarse-grained sediments, coral gravel, and cobbles, to separate them from simple sand cays. On the other hand, Richmond (1993) uses the more general meaning of *motu* to mean any atoll islet or island. Note that in New Zealand

Maori language *motu* is not limited to an islet or island, but can also refer to any land, clump of trees, ship, or anything else that is separated or isolated.

## Classification of atoll islands

There have been several classifications of reef islands (see *Coral Cay Classification and Evolution*) and these can be equally applied to islands on atolls. However, there are two well-known classifications specifically for atolls. The first by MacNeil (1972) who classified atoll islets “according to the way they are formed” noting that most atoll islands in the northern Marshall Islands are accumulations of sediments around obstructions of rock, the most common obstructions being platforms of raised reef, storm rubble tracts, and beach rock. Hence, three main types are distinguished:

- Type 1 islets are formed on platforms or eroded remnants of raised reef
- Type 2 islets are formed on rubble tracts of storm-cast debris
- Type 3 islets are formed from consolidated sand bars or beach rock

Special islets, including combinations of the above, were recognized as the fourth type.

More recently, Richmond (1993) distinguished four types of atoll islets based on morphology, sediment and rock characteristics, and position on reef rim from observations in western Kiribati, Tuvalu, and the Cook Islands:

- Type 1 islets are analogous to sand cays and occur primarily adjacent to reef passages on the leeward rim or atop lagoon patch reefs
- Type 2 islets are typically U-to-boomerang shaped and develop on high energy complex bends of the atoll rim
- Type 3 islets are narrow, elongated gently curved to sinuous in plan shape, and are composed primarily of several parallel ridges which are often separated by a central depression.
- Type 4 islets are complex landforms developed around cemented rubble and reef flat deposits and exhibit a wide variety of shapes.

This last class of islets corresponds closely to the first two islet types of MacNeil’s classification above.

In addition to these scientific classifications, most atoll states and communities have local words or terms to describe the range of typical islands in their territories. Thus, in the Maldives, island classification is based on the presence or absence of vegetation, typical sediments, and relative size. Large vegetated sand islands are known as *raa* and smaller ones as *fushi*. *Huraa* are vegetated shingle or rubble islands. Unvegetated islands include *finolhus* for sand cay/banks and *huraagandu* or *huraalette* for shingle cay/banks. Throughout much of Polynesia, prefixes or suffixes provide further descriptions of atoll *motu* such as *Motu-iti* = small island, *Motu-one* = sand island, *Motu-loa* = long island, and *Tua-motus* = islands on the ocean’s back.

## Geomorphic features of atoll islands

Regardless of island size or shape, and despite their low absolute elevation, atoll islands possess subtle but recognizable variations in surface topography which reflect both geomorphic processes and sediment types. Three natural landform units can often be distinguished: a high-gravel ridge or ridges on the ocean or windward side; a low-sand flat ridge or ridges on the lagoon or leeward side; and a central depression or flat between the two. This asymmetric topographic form is also present on islands comprising a single sediment type, either sand or gravel. However, on islands located in environments where there is no clear windward or leeward side, islands are commonly basin shaped with a high peripheral ridge of roughly equal elevation encircling the whole island. Classic examples of this topographic form occur on the circular patch reefs within lagoons of Maldivian atolls.

On most atoll islands the highest natural elevation is the wave-emplaced ocean side or peripheral beach ridge, which commonly reaches 3–4 m above MSL. On some islands, however, the beach ridge is topped by a dune of fine wind-blown sand, although the presence of sand dunes is not a usual feature on most atoll islands. Where dunes do occur they reach higher elevations than wave-formed ridges, on *Cocos (Keeling) Islands*, up to 5.5 m above MSL on Home Island, 7 m on West Island, and 11 m on South Island (based on surveys reported by Woodroffe and McLean (1994)).

Excluding sand dunes, the highest elevation on atoll islands, and often the greatest and most complex relative relief, results from human activity rather than natural processes. From French Polynesia in the Pacific to the Laccadive–Maldivian archipelago in the Indian Ocean, crop cultivation, especially for taro and banana, is universally carried out in flat-floored depressions or pits excavated down to the island water table. Spoil dug from the pit is dumped around the pit edge building a spoil bank above the level of the surrounding land. The resulting topography is frequently chaotic, especially where groups of pits and banks occur in close proximity to one another.

## Sediments, soils, and groundwater

Atoll islands are made up of calcareous sediments, primarily the skeletal remains of organisms living on the adjacent reef or in the lagoon. Invariably, the coarsest materials comprise whole or broken clasts of coral, typically of sizes from a few centimeters to a few decimeters. In contrast to this single taxa dominance in the gravel and rubble fraction, sand-sized sediments may include small coral fragments, but more commonly comprise a mix of coralline algae, mollusks, foraminifera, and *Halimeda*. Both the calcareous and textural characteristics of the sediments have a major influence on soil properties. Not surprisingly, atoll soils tend to be light colored, shallow, alkaline and coarse textured with no clay. Fertility is highly dependent on the organic matter

content primarily from vegetation and leaf litter, and moisture retention is generally low. Atoll soils are also excessively well drained; water from rainfall quickly percolates to the water table. Fresh water generally tops the groundwater lens within atoll islands, beneath which is the denser saline water originating from the surrounding ocean and lagoon. Traditionally, the fresh water lens has been used as the primary source of potable water by atoll communities.

## Processes of formation and change on atoll islands

Islands accumulate on atoll reefs where sediment is available and where wave processes are focused, often as a result of wave refraction around the reef. Frequently, island shape mimics that of the reef, several examples from Tuvalu being cited by Richmond (1993). Whether or not islands will form on atoll reefs is also dependent on the strength of wave energy. A west to east traverse across South Maalhosmadulu atoll in the Maldives shows that continual high wave energy on the western reef rim sweeps sediment right across the reef platform and islands only occur on the broadest reef flats. In contrast, on the eastern atoll rim where wave energy levels are lower, islands occur on most of the available reef platforms. The more equal and lowest magnitude wave energy of the central atoll ensures mobile sediments are trapped on reef tops, the resulting islands occupying a large proportion of the available reef surface (Kench et al., 2006).

Catastrophic storms have also been regarded as a primary mechanism in the initiation of atoll islands and especially *motu* as recognized in the classifications of MacNeil (1972) and Richmond (1993) outlined earlier. The hurricane/typhoon hypothesis of island formation has a long history with strong support from some of the greatest late nineteenth- to early twentieth century reef scientists based on observations particularly in the *Cocos (Keeling) Islands* and *Funafuti Atoll*. Modern analogues of the delivery of large masses of coral debris to reef surfaces by tropical storms abound; the massive rubble banks formed during Typhoon *Ophelia* at Jaluit atoll in January 1958 and Hurricane *Bebe* at Funafuti in October 1972 provide two excellent examples. Indeed, as MacNeil (1972) and many others have noted, without storms most islets would not be built, and because of storms some islets become larger, while others are reduced or disappear. One implication of this is that sediment delivery is episodic, a point stressed by Wood-Jones (1912: 261) who based on his experience on Cocos (Keeling) proposed a “law of atoll growth” stating that “the processes of formation take place in fits and starts.”

A more critical assessment of the role of episodic storms and fair weather periods was developed by Bayliss-Smith (1988) who modeled the difference in response between gravel *motu* and sand cays on Ontong Java atoll, Solomon Islands. Storms result in a net input of coarse rubble on *motu*, but they cause shore erosion

on sand cays. During subsequent fair weather, storm rubble is redistributed on *motu*, while sand cays recover from the erosional episode and buildup between storms. Bayliss-Smith's model has proved a robust one and has been modified and expanded by several other researchers.

In contrast to the well-documented impacts of tropical storms on atoll island construction and destruction, the impact of tsunami is more ambiguous, even though atoll islands throughout the Indo-Pacific region must have been subject to multiple tsunami during their geological histories. Few investigations of the impact of tsunami on atoll islands have been made, the Sumatran tsunami of December 26, 2004 being a notable exception with several studies of its effects on the Maldives. While the tsunami had tragic consequences for many inhabited islands in the Maldives, pre- and post-tsunami geomorphic surveys on a number of uninhabited islands showed both erosional and depositional changes, little major damage, and a net long-term effect favoring island accretion rather than reduction (Kench et al., 2008).

### Stabilization processes

Once formed, atoll island deposits can be stabilized by a number of different processes including colonization by terrestrial and littoral vegetation and lithification of island and beach sediments. Vegetation, through root binding and the accumulation of humus, stabilizes land surfaces and enables soil formation to proceed, while along island margins root masses of coconut palms, pandanus, and broadleaf trees often form conspicuous "phyto-revetments." Island shores can also be protected by a fringe of intertidal mangroves or *Pemphis* that serve to slow down particle movement and entrap sediment.

Lithification of unconsolidated deposits can also take place, both within islands and around their margins. Examples of the former include the formation of phosphate rock and cay sandstone (*Phosphatic Cay Sandstone*), while beach rock and beach conglomerate (*Conglomerates*) or breccia are common littoral rocks, which give an island some resistance. Both form natural sea walls and groynes and serve to protect an island from erosion. They can also form a locus for island accretion, and are included in MacNeil's classification of atoll islets (Types 1 and 3) and that of Richmond (Type 4).

### Origin and development of atoll islands

Islands on sea-level atolls are geologically young, having developed only in the last few millennia (mid-late Holocene). Obviously, island accretion postdates the surfaces on which the islands are built, be that surface conglomerate platform, solid reef flat, or lagoonal sediment. Many researchers have suggested that the formation of islands on atolls was triggered by a slight fall in sea level from a mid-Holocene high stand. Such an interpretation has been advocated for a large number of atolls extending from the southernmost atoll in French Polynesia (Temoe)

through the Tuamotu archipelago and Cook Islands in the Pacific to Cocos (Keeling) Islands in the eastern Indian Ocean, where the majority of islands are perched on a conglomerate platform or emergent reef flat (Woodroffe and McLean, 1994). On the other hand, there is evidence to indicate that some atoll islands accumulated earlier, when sea level was rising rather than falling, as demonstrated by Kench et al. (2005) for islands in South Maalhosmadulu atoll in the central Maldives.

It is evident from this analysis that there are several ways in which atoll islands can form, including through storm wave action, and that they have formed at different times over the last few millennia (McLean and Hosking, 1991). Moreover, some islands may have developed episodically and others incrementally. Woodroffe (2000) has proposed a number of different scenarios to illustrate chrono-sequences of island accumulation such as accretion away from a central core, progradation in a lagoonward or oceanward direction, or through sediment rollover or overwash. More recently, quantitative models using morphodynamic principles have been used to test field-based models and to suggest that there is a growth-limiting size to atoll islets (Barry et al., 2008).

### Future status of atoll islands

Due to their small size, low elevation, and reliance on locally generated reefal sediments, atoll islands are considered particularly vulnerable to the effects of climate change and especially sea-level rise. The principal impacts from sea-level rise are expected to include: shoreline erosion, inundation and flooding, and saline intrusion, the consequences of which may be to reduce island size, waterlog low-lying areas, and contaminate fresh groundwater supplies. Given these potential impacts, it is surprising so little substantive research has been done on these issues in the atoll world. However, the research that has been done suggests that atoll islands may be much less vulnerable than portrayed in the media or by atoll governments. Geomorphic studies such as the recent comprehensive analysis by Woodroffe (2008) indicates that atoll islands exhibit a degree of physical resilience, that sea-level rise is not the only climate change issue of relevance to atoll islands, and that the key message is that islands will differ in their susceptibility to sea-level rise. Woodroffe's conclusion reiterates an earlier comment by Richmond (1993: 1193) that even within an atoll "different islet types could respond differently to such climate changes as sea-level rise and increased (or decreased) storminess."

Finally, it is interesting to recall that nearly 50 years ago Wiens (1962: 135) wrote about the fate of atoll land with rising sea levels as follows: "In the next 5,000–6,000 years it is possible that periods of rising sea levels may inundate most present land on atolls and possibly destroy most present reef islets." Perhaps Wiens' time scale is an order of magnitude or two out as we may already be in one of those "periods of rising sea levels."



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## Cross-references

Atolls  
 Cay Formation  
 Cocos (Keeling) Islands  
 Coral Cay Classification and Evolution  
 Coral Cays-Geohydrology  
 Coral Cays, Vegetational Succession  
 Enewetak Atoll, Marshall Islands  
 Funafuti Atoll  
 Maldives  
 Mururoa Atoll  
 Shingle Ridges  
 Soils of Low Elevation Coral Structures  
 Vegetated Cays  
 Wave Shoaling and Refraction

## ATOLLS

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## Definition

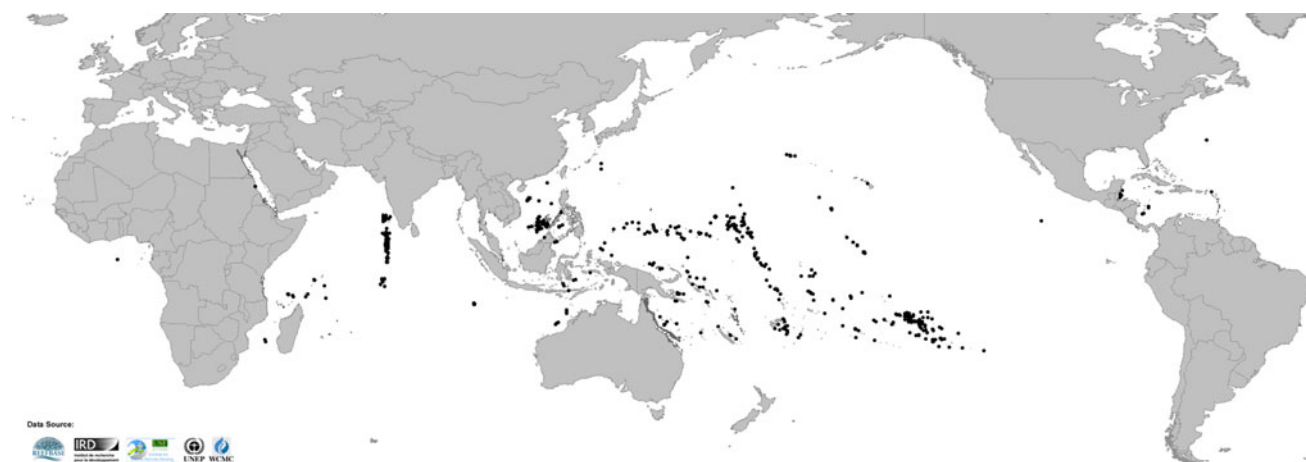
Atolls are annular mid-ocean reefs; the reef rim supports isolated, or near-continuous, reef islands composed of un lithified or poorly consolidated sand or gravel, and encloses a central lagoon.

## Introduction

The term “atoll” is derived from a Maldivian (divehi) word, *atolu*. Atolls are ring-shaped reefs that occur in mid-ocean, often in linear island chains or archipelagoes. The most extensive groups of atolls occur in the Pacific Ocean but there are also numerous atolls in the central Indian Ocean (Figure 1). The reef platforms that form atolls are generally characterized by reefs that reach sea level, especially on the windward margin of the reef platform, although there is considerable variation in the extent to which the reef crest is continuous around the entire perimeter of the central lagoon. There are several hundred atolls which occur across a wide range of climatic and oceanographic conditions (Bryan, 1953), and show a wide variety of shapes (Stoddart, 1965; Shimazaki et al., 2006).

Although there is consensus that many mid ocean reefs are atolls, it is more difficult to settle on an unambiguous definition of what constitutes an atoll. The scientific study of atolls owes a considerable debt to Charles Darwin, first because of his insight into reef development and the evolution of atolls, but also because he produced a map of the distribution of known atolls, as well as other reef types, which focused on the geological factors related to where atolls have formed.

Definitions of an atoll vary, but emphasize several factors in common. Shepard considered an atoll: “an oval-shaped coral reef surrounding a lagoon in which there are no islands other than slightly emerged reefs or small sand cays” (Shepard, 1948, p. 251). Wiens, in his book on atolls, suggested that atoll shape is too irregular to be captured by this definition, and believed that the definition by Kuenen is preferable: “all more or less continuous reefs surrounding a distinctly deeper lagoon with or without lagoon reefs... which rise from a sea bottom which is too deep for the growth of coral reefs” (Newell and Rigby, 1957, p. 21, following Kuenen). Wiens proposed his own definition: “an atoll is a more or less continuous emerged or slightly submerged calcareous reef surrounding a distinctly deeper lagoon or several such lagoons without emerged volcanic islands, which stand apart from other islands, and whose upper seaward slopes rise steeper than the repose angle of loose sediments from a generally volcanic foundation too deep for the growth of reef corals” (Wiens, 1962, p. 8).



**Atolls, Figure 1** The global distribution of atolls, map produced courtesy of Reefbase (<http://www.reefbase.org>).

Although most atolls have a lagoon, sheltered from open ocean swell by the peripheral reef, there are also numerous small platforms, which instead of a lagoon, may be dominated by a single island in the middle of these smaller platforms. These are generally called table reefs, following Tayama (1952), and on those where an extensive reef-top island has formed there is often a swampy central depression.

In the Pacific Ocean there are more than 80 atolls in French Polynesia, most in the Tuamotu Archipelago (Agassiz, 1903a; Guilcher, 1988). There is a prominent chain of atolls that used to be known as the Gilbert and Ellice islands; the Ellice Islands now form Tuvalu. The Gilbert chain is now part of Kiribati; it comprises a sequence of atolls (Richmond, 1993), and there are additional atolls in the Phoenix and Line groups (Keating, 1992). Atolls are extensive through the Marshall and Caroline Islands, with several other atolls in the Federated States of Micronesia. Many of the Cook Islands are atolls, and three atolls comprise Tokelau. The northernmost atoll is Kure in the northwestern Hawaiian Islands at 28°45'N (Riegl and Dodge, 2008). The southernmost is Ducie Island in the Pitcairn Islands group (24°40'S), although Elizabeth Reef in the Tasman Sea at 29°58'S is further south, but may not be a true atoll as it might have formed over a truncated volcanic basement (Woodroffe et al., 2004).

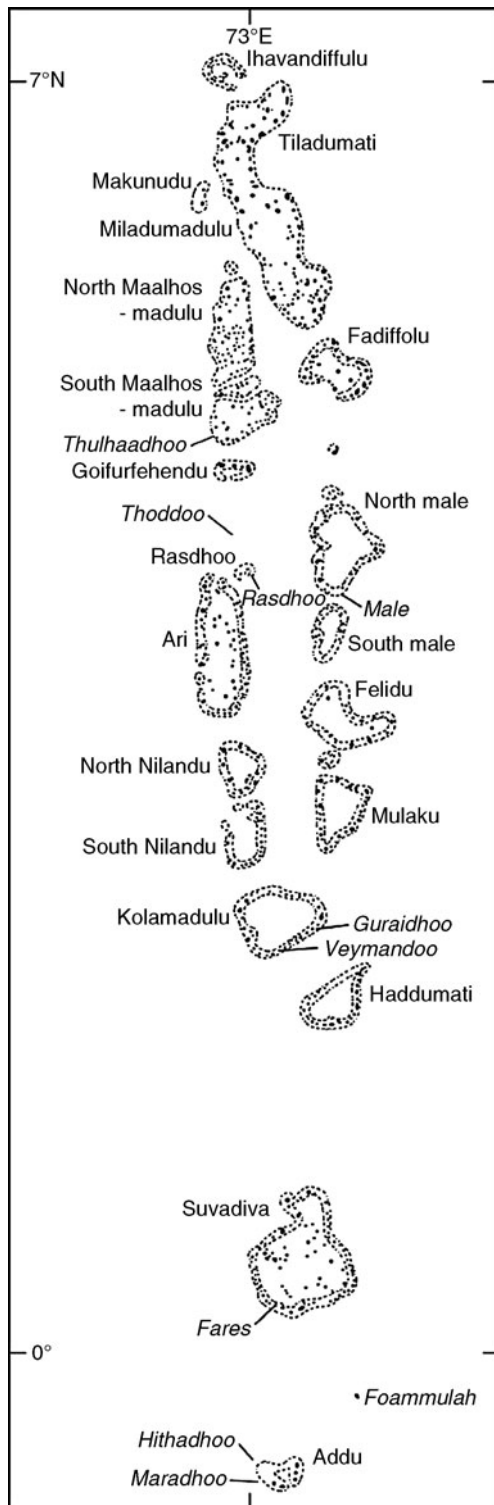
In the Indian Ocean, the Maldives comprise a double linear chain of atolls (Figure 2). The Maldives were the subject of detailed descriptive accounts by Alexander Agassiz (1903b) and Stanley Gardiner (1903). This chain extends through the Laccadives (Lakshadweep) Islands to the north, as a single chain. Minicoy, which was described in detail by Gardiner in his descriptions of Maldivian reefs (Gardiner, 1903, 1931), is the southernmost of this group which has received much less study (Siddique, 1980). A more variable group of reefs comprises the Chagos

archipelago to the south (Sheppard and Seward, 1999). There are outlying atolls in the Seychelles and southwest Indian Ocean (Stoddart, 1973a), and the Cocos (Keeling) Islands in the eastern Indian Ocean (Woodroffe and Berry, 1994).

Atolls are relatively rare in the Caribbean; Stoddart (1965) suggested that there were 27, but Milliman (1973) considered only 10 to be atolls. Reefs such as Hogsty Reef in the Bahamas and Roncador Bank off the east coast of Nicaragua have been described as atolls; however, they clearly differ in origin and morphology from Indo-Pacific atolls. Three atolls have been described just east of the Belize barrier reef (Stoddart, 1962; Gischler, 1994).

The largest atoll is Suvadiva (Huvadhu) in the Maldives with an area of 2,800 km<sup>2</sup>; the largest land area is on Christmas Island (Kiritimati) in Kiribati with an area of 321 km<sup>2</sup>. Raroia in the Tuamotu has a lagoon area of 171 km<sup>2</sup>. Kwajalein measures 120 by 32 km, Rangiroa 79 by 34 km, and Tijger, south of Sulawesi, 72 by 36 km.

There are several types of atoll. Atolls can be classified into ocean atolls and shelf atolls (Ladd, 1977). The ring-shaped reefs in open ocean, which we now realize to be in a mid-plate setting, were mapped in detail by Darwin and are unambiguously atolls. However, there are several other groups of islands that contain reefs that have been classified as atolls. For example, the numerous reefs of the Indonesia archipelago contain some of the most diverse of island groups (Kuenen, 1933). At least 55 are considered atolls by Tomascik et al. (1997). There are also a series of reefs in the South China Sea, where three types of atolls have been recognized: ocean atolls, shelf atolls, and slope atolls (Wang, 1998). Whereas the South China Sea islands include true oceanic atolls, such as Scarborough Reef (Huangyan Dao, Wang et al., 1990), those further north are shelf atolls and there are also a series of 70 continental slope atolls in intermediate water depth.



**Atolls, Figure 2** The Maldivian archipelago which for much of its length comprises a double chain of atolls, but reduces to single reef platforms to the south.

Although shelf atolls are also found elsewhere, such as off the northern coast of Australia (e.g., Rowley Shoals and Seringapatam Atoll on Timor Shelf, see *Western Australian Reefs*), slope atolls have rarely been described.

A further variant of an atoll is a reef called an almost atoll. This term has been used differently by different authors; sometimes it has been used to refer to a rapidly subsiding volcanic island that did not form an atoll. However, it is generally taken, in the sense used by Davis (1928), to refer to a residual volcanic island that is surrounded by an annular reef, and which will be an atoll when the remaining volcanic rock has subsided below the level of the sea. Chuuk (Truk) is a classic example, but Aitutaki is an almost atoll in the southern Cook Islands, which has been described in detail by Stoddart (1975).

There has also been recognition of a class of bank atolls, sometimes referred to as submerged atolls, that includes banks on which reef growth does not reach sea level. There are examples in Palau and the Caroline Islands, and Saya de Malha in the Indian Ocean. A further category comprises atolls that are “raised” or emergent, in which older limestones are exposed. Reef limestones of last interglacial age have been found to underlie the rim of atolls at depths of 10–20 m (described below), and on several atolls these outcrop at the surface, or as in the case of Aldabra and Henderson Island, are the dominant subaerial limestone (Braithwaite et al., 1973; Pandolfi, 2008). Elevated atolls include Maré, Lifou and Ouvea in Vanuatu, Makatea in French Polynesia, Nauru, and Niue. Older limestones record successive periods of accretion, and many of these limestones are dolomitized or contain phosphate deposits that have often been mined. Mataiva in the Tuamotu Archipelago also has exposures of Tertiary limestone.

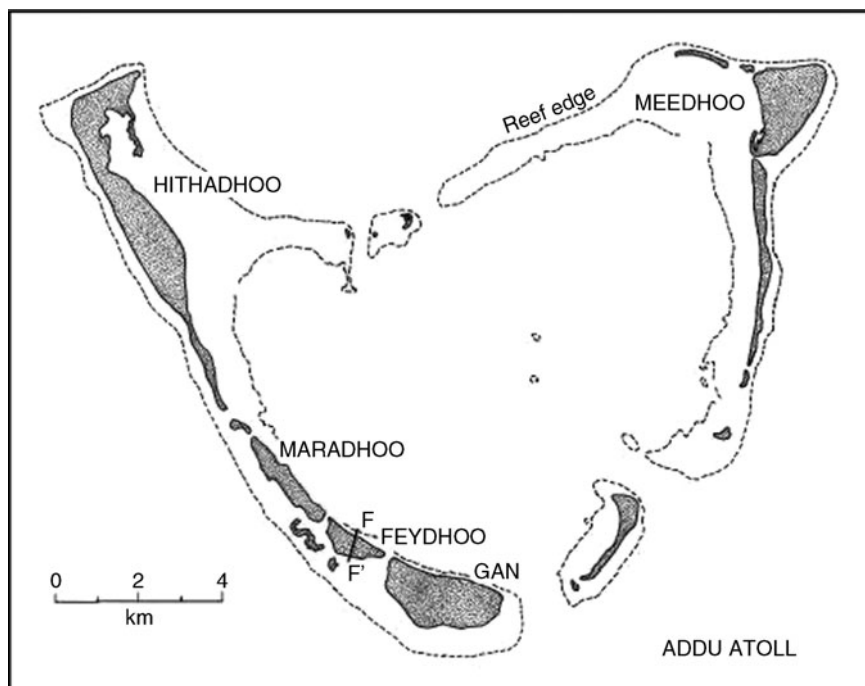
### Surface morphology

The general topography and geomorphology of atolls was outlined in a book by Wiens, entitled *Atoll Environment and Ecology*, based on detailed studies sponsored by the Pacific Science Board and focused on the Marshall Islands, as well as selected other Pacific atolls (Wiens, 1962). In this account, and in a major review by Stoddart (1969), three features are distinguished: the outer reef, the reef rim, and the lagoon. These are considered below.

### Outer reef

The outer reef of an atoll is near continuous and is generally subject to ocean swell that breaks on all sides (Figure 3). The windward rim of the atoll is generally more continuous than the leeward; for example, the major passages through the reef and into the lagoon are more often on the leeward side of the atoll, as seen in the Tuamotu Archipelago (Guilcher, 1988). In many cases, reef islands are more abundant on the windward reef than on the leeward. In the case of many of the atolls in Kiribati, the leeward margin does not reach sea level, and many





**Atolls, Figure 3** Addu Atoll, the southernmost of the Maldives, showing a near continuous rim around the more exposed margins.

of the larger atolls, such as Tabiteuea and Tarawa have a much better developed eastern windward margin (see Figure 4).

The reef front is steep and rises abruptly from the ocean floor, often from as deep as 4,000 m. Although there is a rain of sediment sourced from the living reefs that cascades down the forereef, many atolls margins are characterized by a steep drop-off which exceeds the angle of repose, indicating that the reef has been built by vertical accretion. Much of the forereef of Mururoa (*Mururoa Atoll*), below 10 m water depth, is at an angle of 45° (Chevalier et al., 1969).

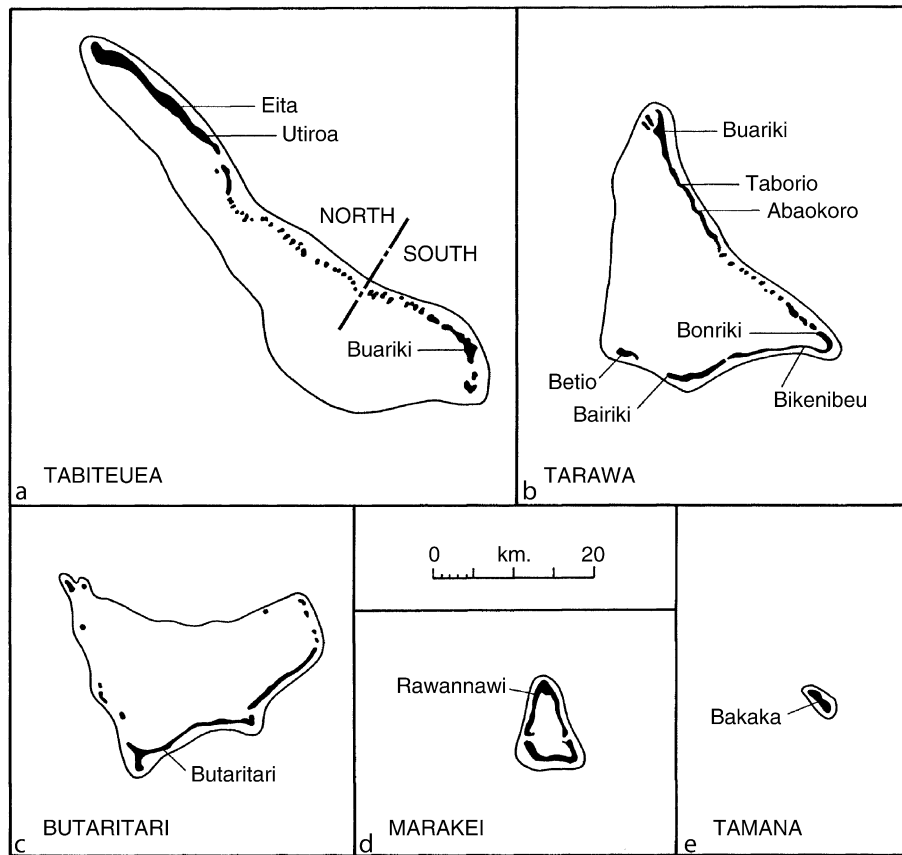
The reef front often has one or more distinct terraces; for example at 15–20 m depth on the reef front of Marshall Island atolls (Emery et al., 1954). The shallow reef front commonly has a prominent spur and groove (*Spurs and Grooves*) morphology (Munk and Sargent, 1954). This consists of broad ridges, covered by coral or coralline algae, which run at right angles to the reef margin, oriented into the dominant wave direction. The ridges are interpreted as constructional, interspersed with sand-filled channels that may be erosional. Spur and groove are best developed on high-energy reef fronts and merge into surge channels at the reef crest (see *Reef Front Wave Energy*).

The reef crest is generally dominated on the windward side of the atoll by a prominent crest, veneered by pink algae (*Porolithon* or *Lithothamnion*) forming an algal rim (*Algal Rims*) on higher-energy trade-wind dominated windward reef crests. Waves break on all sides of an atoll, if the reef reaches sea level, but the largest breakers are on the margin that faces the swell direction.

#### Reef rim

The reef rim can be of variable width and contains islands in some instances, or can be a broad reef flat in others. Typically, the reef flat (*Reef Flats*) is between 100 and 1,000 m wide; many of the north Pacific atolls have an average width of about 500 m (Wiens, 1962). The reef flat is shallow, or commonly much of it may be exposed during lowest tide. In other settings, distinct zones can be discriminated across the upper surface. The algal rim, over which coralline algae are dominant, often merges into a backreef zone that has detrital material on its surface. In the higher energy setting, this is a discontinuous scatter of boulders of dead and detached corals, or fragments of reef limestone. In less exposed sites, such as lower energy atolls rims or the leeward margin of otherwise high-energy atolls, the fragments are smaller and less frequent. Corals thrive in pools of water that remain deep enough over a tidal cycle, and the reef crest and immediate backreef are some of the most productive settings. Turf algae can be abundant and benthic foraminifera are epiphytic on these algae or under loose boulders and within crevices on the reef (Collen and Garton, 2004).

The reef flat that forms on Pacific and Indian Ocean atolls is usually broad and flat. On some atolls a slightly deeper channel may occur behind the boulder zone, usually with thickets of branching *Acropora* and *Montipora* corals, and this has been called the boat channel (*Boat Channel*) as it is adopted as the preferred route to navigate a small boat along the reef rim. If the reef flat is at an elevation that it is exposed during low tide, then the surface is

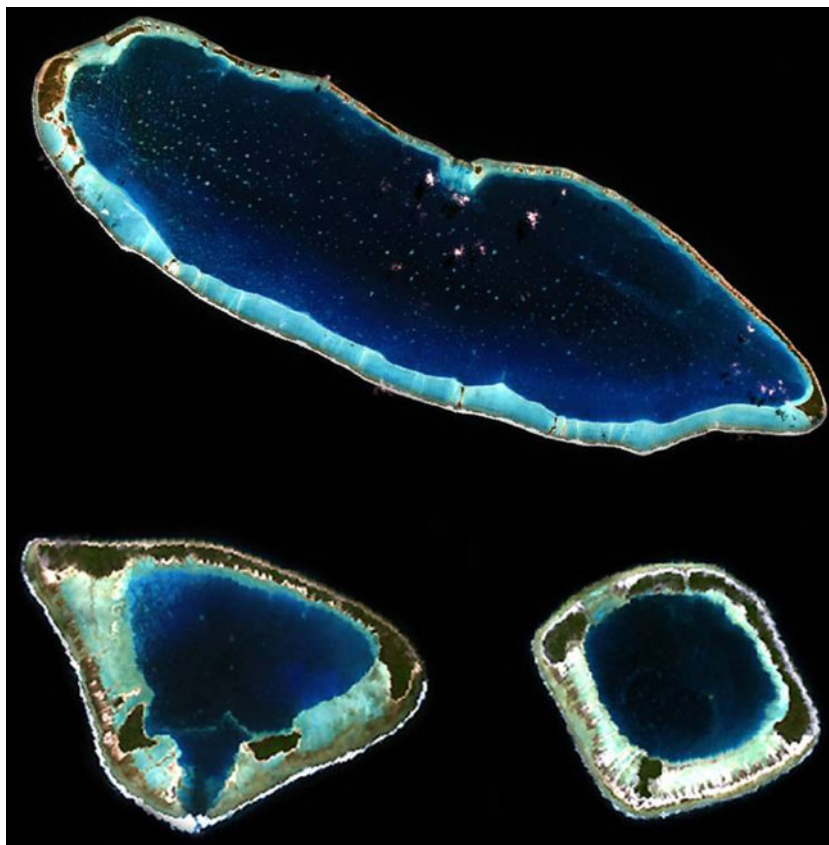


**Atolls, Figure 4** Several of the atolls in the Gilbert chain, Kiribati, showing a selection of atoll outlines. Tamana is an example of a table reef on which there is a single island on a smaller reef platform.

generally veneered by coralline algae, but deeper pockets enable corals to persist. Where there is sufficient water over the reef top for them to establish, massive corals, particularly of the genus *Porites*, are often limited in their upward growth by exposure during low tide and adopt a microatoll growth form. These microatolls (*Microatoll*) can grow laterally in some cases to several meters diameter. There is also often the distinctive blue octocoral *Heliopora* in this setting. The elevation of the reef flat is critical in determining whether there is suitable substrate for coral to establish, and, as will be discussed below, slight changes of sea level can alter the nature of the habitat on the reef flat. In many cases the reef flat can be interpreted to have formed under a slightly higher sea level, and the gradual fall of sea level over recent millennia has resulted in substrates on which coral previously grew, now being emergent at low tides and no longer suitable for modern corals to colonize. Aerial reconnaissance often reveals a backreef zone that appears aligned, with linear reef-crest normal stripes extending into the lagoon. Whereas this aligned coral zone (*Boulder Zone/Ramparts*) suggests a response by corals to the directions of flow across the reef, such patterning is rarely apparent when actually on the reef flat.

In a number of cases, evidence of a higher former sea level can be seen, such as fossil corals in their growth position (including microatolls that grew at an elevation at which they can no longer grow). On a few atolls mushroom shaped rocks indicate that such a higher surface is being actively undercut (e.g., Mopelia Atoll in the Society Islands), although in a few cases in the Tuamotus these older remnants, termed *feo*, are Pleistocene in age. On a few atolls there is also a fossil algal ridge stranded several hundred meters inshore of the modern algal rim. Fossil algal rims of late Holocene age have been dated on Suvarrow Atoll in the Cook Islands (Woodroffe et al., 1990a) and Nukutipipi Atoll in the Tuamotus (Salvat and Salvat, 1992).

Reef islands develop on many of the reef rims of atolls. The details of these islands are examined below, but one of the most significant features is the degree of continuity along the reef. Where there are no islands, the reef flat extends from reef crest to lagoon. Major passages into the lagoon are significant because they enable significant water exchange between ocean and lagoon; they also interrupt the chain of islands along the rim. The Polynesian term for large and deep passages is *ava*. Smaller and shallower passages between islands are called *hoa* (Figure 5).



**Atolls, Figure 5** Three atolls in the Tuamotu. The *upper* is Kaukura Atoll which is about 48 km from west to east; the *lower*, Haraiki and Tauere Atolls, are both about 7 km from west to east (satellite imagery courtesy of Serge Andréfouët).

The degree to which the lagoon of an atoll is enclosed, and the nature of the passages is a key feature in relation to circulation in, and flushing of, the lagoon (see [Lagoons](#) and [Lagoon Circulation](#)).

Those atolls with numerous or large *ava* are generally effectively flushed by tidal circulation, whereas atolls that have almost continuous reef rims around their perimeter (see Tauere Atoll, [Figure 5](#)) are more likely to be flushed through the action of waves overtopping the reef rim (Callaghan et al., 2006). The nature of flow, and the degree to which sediment is transported through inter-island passages (*hoa*), varies as a function of depth, distance from the reef crest, and tidal and wave energies. Similar passages occur between islands on the rim of Indian Ocean atolls. For example, Guppy (1889) made important observations in the passages that feed the lagoon on the Cocos (Keeling) Islands on the basis of which he made a first estimate of the rate of sediment infill, inferring that the lagoon would require several thousand years to fill with sediment. The significance of these interisland passages has been further examined by Kench and McLean (2004).

Where *hoa* do connect with the lagoon, they can be conduits for sediment transport and a sand apron, comprising material sourced from the reef or reef flat, which

accumulates at the lagoonward mouth of the *hoa*. In atolls that have a large enough lagoon that sufficient wave energy can be generated across the lagoon, these sediments can be further reworked alongshore along the reef island lagoon shores, such that a spit can form, in some cases closing the *hoa* and forming a closed pond known in Polynesia as *tairua*; an example of an atoll where this has happened is Taiaro.

Sheltered locations on the lagoonal shore may be colonized by mangroves; several species of mangroves occur on atolls in the Maldives, and in the Marshall Islands, Kiribati and Tuvalu. Mangroves are absent from the Cook, Tokelau and Tuamotu islands, although introduced to the Society Islands. Mangroves decrease in species abundance from west to east across the Pacific although with a disjunct species *Rhizophora samoensis* occurring from New Caledonia to Samoa (Woodroffe, 1988).

### Lagoon

The lagoon is sheltered in comparison to the outside of the atoll, and may contain scattered patch reefs, which have also been called pinnacles or knolls. Some lagoons



(*Lagoons*) may have few such patch reefs, but in other atolls there can be an intricate mesh of reefs forming a reticulate network of shallow reefs, such as Mataiva (see also *Reticulated Reefs*). The narrow ridges of reef separate deeper holes, termed “*Blue Holes*”. Lagoons vary considerably in depth; they can be shallow, or tens of meters deep (Gischler, 2006). Reginald Daly believed that there was an overall similarity in the depth of many atolls, which he considered provided support for his theory of glacial control (described below, see also Daly). However, it is now recognized that there is considerably more variation in depth than envisaged by Daly. Atolls in the southern Maldives, for example, contain lagoons that are more than 70 m deep, but other lagoons may partially dry at low tide (the southern end of the lagoon of the *Cocos (Keeling) Islands*, for example).

The lagoon is a prominent feature of most atolls. Lagoons are gradually infilling both with sediment produced within the lagoon, but more especially with sediment derived from the more productive reef rim. Purdy and Gischler (2005) propose an “empty bucket” model of lagoon infill, capturing the stages of infill after the surrounding reefs have caught up with sea level (Neumann and Macintyre, 1985). The pattern of infill is likely to depend on the nature of the reef rim, and sediment production may be proportional to the atoll’s perimeter (Tudhope, 1989).

The lagoon at Enewetak has been described in a detailed study by Emery et al. (1954). It reaches a depth of 55 m, and the benthic communities form a series of concentric zones (Colin, 1986), with foraminifera a conspicuous component of lagoon sediments, and a patch reef zone (termed knolls or pinnacle reefs by Emery) (Wardlaw et al., 1991). Similar concentric zones are known to occur in the sediments of Rongelap and Bikini Atolls (Emery et al., 1954) and also in the case of Kapingamarangi Atoll (McKee et al., 1959). More recent studies reaffirm the significance of foraminifera, particularly *Calcarina* and *Heterostegina* in each of Kayangel in the Palau Islands, and Enewetak and Majuro in the Marshall Islands (Yamano et al., 2002). There is much variability in the lagoon floor sediments of Tarawa Atoll, in Kiribati, but foraminifera are a prominent component (Weber and Woodhead, 1972; Lovell, 2000; Paulay, 2001). The calcifying alga *Halimeda* is one of the most prominent features of the sediments of some of the deeper lagoons; it dominates much of the interior of the lagoon of Suvarrow (Tudhope et al., 1985). In the case of Cocos, much of the lagoon is dominated by sediments produced within the lagoon (Smithers et al., 1992). Mud may accumulate in localized embayments within the islands, termed *teloks* on Cocos and *barachois* on Diego Garcia (Stoddart, 1971). On highly enclosed atolls, such as Marakei in the Gilbert chain of Kiribati, lagoon sediment is mud, with reef flat foraminifera found only at the entrance to the narrow reef passage on the eastern margin (Woodroffe, 2008). Mud is typical of the lagoon floor within the reticulated reefs of Mataiva Atoll in French Polynesia (Adjas et al., 1990).

Although active vertical reef growth implies that the reef rim might be a constructional feature, it has been apparent since the study of MacNeil (1954) that solution of the interior of the lagoon occurs during subaerial exposure when the sea is lower than present during glaciations. This view, examined further below in relation to the geological evolution of atolls, has been especially promoted by Purdy and Winterer (2001).

The geomorphology and biogeography of atolls has been mapped in detail where ground reconnaissance has been undertaken, notably through the extensive studies of David Stoddart (*Stoddart, David Ross (1937–)*), or in a few instances where aerial photography is available at suitable scales (Woodroffe and McLean, 1994). Recently, high-resolution satellite imagery has been used in conjunction with state-of-the-art remote sensing algorithms to map reef geomorphology and habitat distribution (Andréfouët et al., 2001, 2003; Naseer and Hatcher, 2004; Yamano et al., 2006).

### Geological evolution of atolls

As the oceans were explored during the seventeenth and eighteenth centuries, atolls became more broadly known. We do not know when atolls first became a feature of familiarity to European explorers, but they have certainly been known since the Spaniard Mendana landed on an atoll in Tuvalu. In the early nineteenth century, Charles Lyell (*Lyell, Charles (1797–1875)*) promulgated the view that atolls represented a coral veneer around the margin of submerged volcanic craters, in his *Principles of Geology* published in the 1830s, a book that was to have a profound influence on Charles Darwin.

Charles Darwin (*Darwin, Charles (1809–1882)*) proposed an alternative theory, his theory of coral reef formation, after witnessing evidence of the vertical movement of land during surveys by *HMS Beagle* on the coast of South America. Darwin’s subsidence theory considered that there “is but one alternative; namely the prolonged subsidence of the foundations on which the atolls were primarily based, together with the upward growth of the reef-constructing corals. On this view every difficulty vanishes; fringing reefs are thus converted into barrier reefs; and barrier reefs, when encircling islands, are thus converted into atolls, the instant the last pinnacle of land sinks beneath the surface of the ocean” (Darwin, 1842, p.109). This remarkable deduction that volcanic islands in mid-ocean might undergo subsidence, and that reefs might proceed through a sequence from fringing reef to barrier reef to atoll, as a consequence of vertical reef growth to sea level, had occurred to Darwin after observing the evidence of uplift in South America, before he ever saw a reef. His hypothesis was reinforced when he viewed the fringing reefs around Moorea from the slopes of Tahiti. Although the *Beagle* passed atolls in the Pacific, it did not stop at any. Darwin wrote the first draft of his theory of reef development as the ship sailed to New Zealand (Stoddart, 1995). The *Beagle* had passed through the Tuamotu Archipelago in what is now French Polynesia, but the only atoll

that Darwin set foot on was the Cocos (Keeling) Islands in the eastern Indian Ocean. Here he keenly accepted observations of the undercutting of coconuts and the erosion of the shoreline as “tolerably conclusive evidence” in support of his theory.

It is important to discriminate that Darwin’s theory applies to the *structure* of reefs, based on their long-term evolution, at timescales of millions of years, whereas the *surface morphology* of the atolls reflects late Holocene formative processes that operate over much shorter timescales (Stoddart, 1973b). Stoddart (Stoddart, David Ross (1937–)) has emphasized the difference in time scale; reef structure (*Reef Structure*) being the outcome of millions of years of geological evolution, whereas the surface morphology results from the most recent (Holocene) adjustments of form to the processes that operate, including subtle changes in sea level. At the time Darwin proposed his theory, the significance of sea-level fluctuations associated with the glaciations was unknown, but it is possible to incorporate our latest understanding of the oscillations of sea level into the gradual formation of the sequence of limestones that underlie a typical atoll.

Darwin’s subsidence theory of atoll evolution was tested by deep drilling on *Funafuti Atoll* in 1896–1898 which, although it failed to reach the underlying volcanic basement, recovered more than 300 m of shallow-water carbonates implying subsidence (Spencer et al., 2008). Subsidence of volcanic basements upon which atolls are founded was eventually substantiated by drilling on the atolls of Bikini and Eniwetak in the Marshall Islands (see a synthesis in Guilcher, 1988, and *Bikini Atoll, Marshall Islands; Eniwetak Atoll, Marshall Islands*). Daly recognized the significance of sea-level fluctuations (Daly, 1934) and documented evidence from across the Pacific that recorded a sea level above present level. However, the *Glacial Control Hypothesis* that Daly advocated to explain reef development, further developed by Wiens (1959, 1962), presumed that reefs were totally planed off at low sea level and that the entire structure of modern reefs was Holocene. The antecedent karst hypothesis advocated by Purdy (1974) corrected this mistaken view, and recognized the significance of *Antecedent Platforms*, often of late Pleistocene age. It has now been widely shown that the reef rim on modern atolls is underlain by older Pleistocene reefs (McLean and Woodroffe, 1994; Montaggioni, 2005).

Darwin’s theory was enthusiastically adopted by several other prominent scientists, most notably Dana (Dana, James Dwight (1813–1895)), and became widely debated. An alternative view proposed by Murray (1889) revolved around a belief that atolls developed as a result of solution of lagoons. Although considered by Gardiner (1931), this view became discredited when it was realized that seawater was supersaturated with calcium carbonate. Wood-Jones (1912) proposed an alternative view based on his time in the Cocos (Keeling) Islands. He thought that it was the production of sediment around the margin of an atoll and its transport and deposition in the interior that prevented coral growth in the center of reef platforms. However, this

sedimentation theory was not widely supported. W.M. Davis (Davis, William, Rorris (1850–1934)), in his review of the origin of reefs (Davis, 1928), considered that the only real contender against Darwin’s view was the glacial control theory proposed by Daly, and in a subsequent review, Cotton (1948) regarded the subsidence, glacial control and antecedent topography theories as plausible.

In addition to his observations on Cocos, Darwin undertook a substantial compilation of information on reefs, and in his book published in 1842, he included a map of the distribution of atolls, which provided further evidence of the fact that most atolls occur in mid ocean (Darwin, 1842).

Further exploration was to extend knowledge about atolls. The distinguished American geologist, James Dana, extended Darwin’s ideas as a result of his visits to Kiribati, Tuvalu, the Tuamotu Archipelago, the Society Islands, Fiji, and the Phoenix and Hawaiian Islands. He was a firm supporter of the subsidence hypothesis (*Subsidence Hypothesis of Reef Development*). Alexander Agassiz (Agassiz, Alexander (1835–1910)) undertook extensive studies of reefs on extended voyages at the turn of the twentieth century. His 9-month cruise on *Albatross* in 1899–1900 enabled him to describe 30 atolls in the Tuamotu Archipelago and 28 in Tuvalu, and the Marshall and Caroline Islands. He followed this with further descriptions of the Maldives Archipelago in 1901–1902, where his observations built on those of Gardiner who had mounted an expedition in 1899–1900. Agassiz attempted to drill Wailangilala atoll in Fiji, but recovered material only from the upper 26 m. The Chagos Archipelago was described during the Percy Sladen expedition, and a fuller account of this period of reef exploration is given by Spencer et al. (2008). The *Cocos (Keeling) Islands* were examined by Guppy (1889); Wood-Jones (1912); and Gibson-Hill (1947), making this one of the best known atolls by mid-twentieth century.

Darwin had realized that drilling through an atoll was the optimal way to test his theory and he wrote before his death to Agassiz in an effort to encourage such drilling (see *Darwin, Charles (1809–1882)*). Such drilling was finally undertaken on Funafuti Atoll. The *Royal Society of London* sponsored a program involving a series of expeditions in the 1890s to Funafuti. The objective was to drill the perimeter of Funafuti to test Darwin’s theory of reef development. The initial fieldwork was led by Professor W. Sollas in 1896; further drilling was undertaken in 1897, together with field mapping by T. Edgeworth David (David, Tannant Edgeworth (1858–1934)) and George Sweet, and the final stage of drilling, although still in shallow-water carbonates, was overseen by Alfred Finckh in 1898. At the time the fact that the core did not reach volcanic basement at more than 300 m depth appeared inconclusive, although it was clear that shallow-water carbonates persisted below depths at which they are now forming. In retrospect we now know from the strontium isotope stratigraphy that dolomite in the lower core was formed through diagenesis between 1 and 2 million years ago. The upper 26.4 m of the core has been radiocarbon

dated indicating a history of sea-level rise during the past 8000 years (Ohde et al., 2002).

During the Quaternary, atolls have evolved in response to a series of sea-level oscillations. It was Daly who gave these Quaternary ice ages such prominence in geological interpretations of oceanic islands. His glacial control theory involved the eradication of coral reefs from areas at their poleward limits, which he called marginal seas during successive glaciations (although this view is not supported by study of reefs at their latitudinal limit). He also believed that the reef rim had been planed off during glacial lowstands, and by inference that the entire reef rim had accreted during the postglacial. Daly's views were further promoted by Wiens (1959, 1962), but are no longer supported (see *Glacial Control Hypothesis*).

Significant further studies on atolls occurred after World War II. American research in the Pacific involved a focus on the atolls of the Marshall Islands. Geological studies were prominent and the stratigraphy of atolls became better known because of selection of sites for atomic bomb testing, as well as through scientific curiosity. Seismic studies in 1946 and 1950 provided the first hint that the carbonates were underlain by volcanic rocks (Raitt, 1954), together with the recovery of noncarbonate rocks dredged from depths greater than 1,400 m on the flanks of these islands. In 1951, drilling on Bikini Atoll encountered basalt at depths of 1,287 and 1,411 m respectively in two boreholes. Examination of the limestones indicated that they had been deposited in shallow water, and the presence of solutional unconformities supported the episodic exposure of these during successive sea-level lowstands (Schlanger, 1963).

Subsequently drilling on Mururoa has revealed 400–500 m of carbonate over the volcanic basement that underlies that atoll (q.v.), with a similar stratigraphy also on neighboring Fangatafu (Lalou et al., 1966). A Quaternary history of the past 300,000 years has been derived (Camion et al., 2001) implying that the atolls became more atoll-like as a result of dissolution of the lagoon and buildout of the periphery through reef growth. On Midway Atoll in the Hawaiian Islands (*Midway Atoll (Hawaiian Archipelago)*), volcanic basement has been encountered at 55 m beneath Sand Island and 378 m beneath reef to the north of the lagoon, further supporting Darwin's subsidence theory (Ladd et al., 1967, 1970).

A series of further studies were initiated by the Pacific Science Board during the period 1946–1969. This included fieldwork on Arno, Ifaluk and Kapingamarangi Atolls in what are now the Federated States of Micronesia, Onotoa in Kiribati, and Raroia in French Polynesia. A compilation of this work led to the publication of the book on atolls by Wiens in 1962. This was also a period during which the Atoll Research Bulletin was initiated (Fosberg and Sachet, 1953; Spencer et al., 2008).

### Quaternary evolution of atolls

Shallower drilling on several atolls has encountered Pleistocene reef limestone, often dated to the Last Interglacial, at

depths of 10–20 m below the modern atoll rim. In the Cocos (Keeling) Islands Pleistocene limestone, shown to be of Last Interglacial age, occurs at depths of 8–13 m below sea level beneath each of the major islands, and seismic reflection profiling records a reflector that correlates with this discontinuity beneath the lagoon (Searle, 1994; Woodroffe et al., 1994). This karstified Pleistocene limestone underlies the rim composed of Holocene limestones. Pleistocene limestone has been shown to underlie the rim of Tarawa Atoll (Marshall and Jacobson, 1985), Funafuti Atoll (Ohde et al., 2002), several atolls in the northern Cook Islands (Gray et al., 1992), as well as atolls in the Maldives and Chagos Archipelagoes (Woodroffe, 2005). In some that have been drilled to deeper depths, such as Eniwetak and Mururoa, it is apparent that the last interglacial limestone is underlain by older reef limestones deposited during preceding highstands (Szabo et al., 1985; Camoin et al., 2001).

When sea level was high during the last interglacial (and presumably former interglacials) an atoll rim similar to the modern existed, although no evidence remains as to whether it contained islands (Perrin, 1990). During glaciation the reef limestones were exposed by the lower sea level, and the emergent limestone underwent solution (karstification). Atolls appear to be undergoing gradual subsidence associated with plate migration (Scott and Rotondo, 1983, see *Subsidence Hypothesis of Reef Development*), so when sea level rose again during postglacial times it flooded the platform around 8000 years ago. There are several atolls on which last interglacial limestone is exposed at the surface (e.g., Aldabra in the western Indian Ocean, Braithwaite et al., 1973; Anaa in French Polynesia, Pirazzoli et al., 1988; and Christmas Island in eastern Kiribati, Woodroffe and McLean, 1998). The extent to which lowering and reshaping of the surface results from subsidence or from solution remains an issue of debate (Purdy and Winterer, 2001, 2006); erosion appears to have accentuated lagoon morphology on many atolls.

### Accretion of the reef rim

Holocene reef growth has been constrained by the pattern of sea-level change; there appears to have been a lag before corals reestablished over the Pleistocene substrate around 8000 years ago. The reef grew in an effort to catch-up with sea level, as revealed in the case of Cocos in the Indian Ocean (Woodroffe et al., 1994) and Tarawa in the Pacific Ocean (Marshall and Jacobson, 1985). After reefs caught up with sea level, lateral progradation of the reef seems to have occurred, particularly in those situations such as Suvarrow and Nukutipi where there are fossil algal rims abandoned behind the modern reef crest.

The majority of polar ice melt appears to have been completed by 6000 years ago, and the volume of water in the ocean at that time is likely to have been similar to that of today. However, hydro-isostatic adjustments mean that the details of relative sea-level history vary geographically (Lambeck, 2002, see *Mid Holocene*). In particular, a fall of sea level occurred relative to far-field



remote islands, which has been termed ocean siphoning (Mitrovica and Peltier, 1991). Whether the sea-level curve at far-field sites peaked abruptly around 6000 years ago and fell since then (through ocean siphoning) or whether there has been post-6000 year melt, with a more gradual peak around 4000 years is difficult to discriminate from atolls, because it was necessary for the reef rim to accrete to sea level before evidence would be preserved (Nunn and Peltier, 2001). The atoll rims have grown from the surface of the Pleistocene limestone to catch up with sea level, so the timing of the initiation of a reef flat in mid Holocene varies geographically from atoll to atoll. Hydro-isostatic adjustments mean that the elevation of mid-Holocene reefs can also vary between atolls.

The conglomerate platform on some atolls contains within it evidence of corals in growth position that formed a part of a former reef flat (see *Conglomerates*). Fossil microatolls are especially useful in this respect, but other reef flat corals such as *Heliopora* can also be important in differentiating units within the conglomerate platform that mark former reef flat surfaces and indicate higher than present sea level, and overlying storm deposits. Radiocarbon dates on corals from conglomerate record inputs of corals detached during storms. For example, ages of 4000–3000 years BP have been obtained on corals from within the conglomerate platform on the Cocos (Keeling) Islands (Woodroffe et al., 1994). Ages from other atolls seem broadly comparable, with evidence for variation in Kiribati-Tuvalu (the Gilbert-Ellice chain), from north (where it may have been as old as 4000 years ago) to south (where reefs may have reached sea level since 2000 years ago, McLean and Hosking, 1991). Radiocarbon ages as old as 5500 years BP have been reported from atoll surfaces in the Tuamotu Archipelago (Pirazzoli and Montaggioni, 1988).

Since the reef rim reached sea level and the reef flat was formed, there has been further carbonate sediment produced which has continued to infill the lagoon (Purdy and Gischler, 2005) and has seen the accumulation of sediments to form reef islands around the margin. Several researchers suggested that island formation on atolls occurred as a result of this slight fall of sea level (Cloud, 1952; Schofield, 1977a, b; Dickinson, 2004).

David and Sweet (1904) undertook mapping of the islands and reef flats around *Funafuti Atoll*, and considered that large *Porites* corals in growth position indicated that the sea had been above its present level relative to the atoll in the past. Similarly Cloud (1952) described outcrops of *Heliopora* in growth position, above the elevation that it presently reaches on the reef flat as evidence of emergence on Onotoa. There has been an ongoing debate about the extent to which conglomerate of this type is formed by storms. An expedition to the Caroline and Marshall Islands (CARMARSEL expedition) specifically to resolve whether the conglomerate was a storm deposit or as an indicator of higher sea level reached no consensus (Shepard et al., 1967; Newell and Bloom, 1970). The most

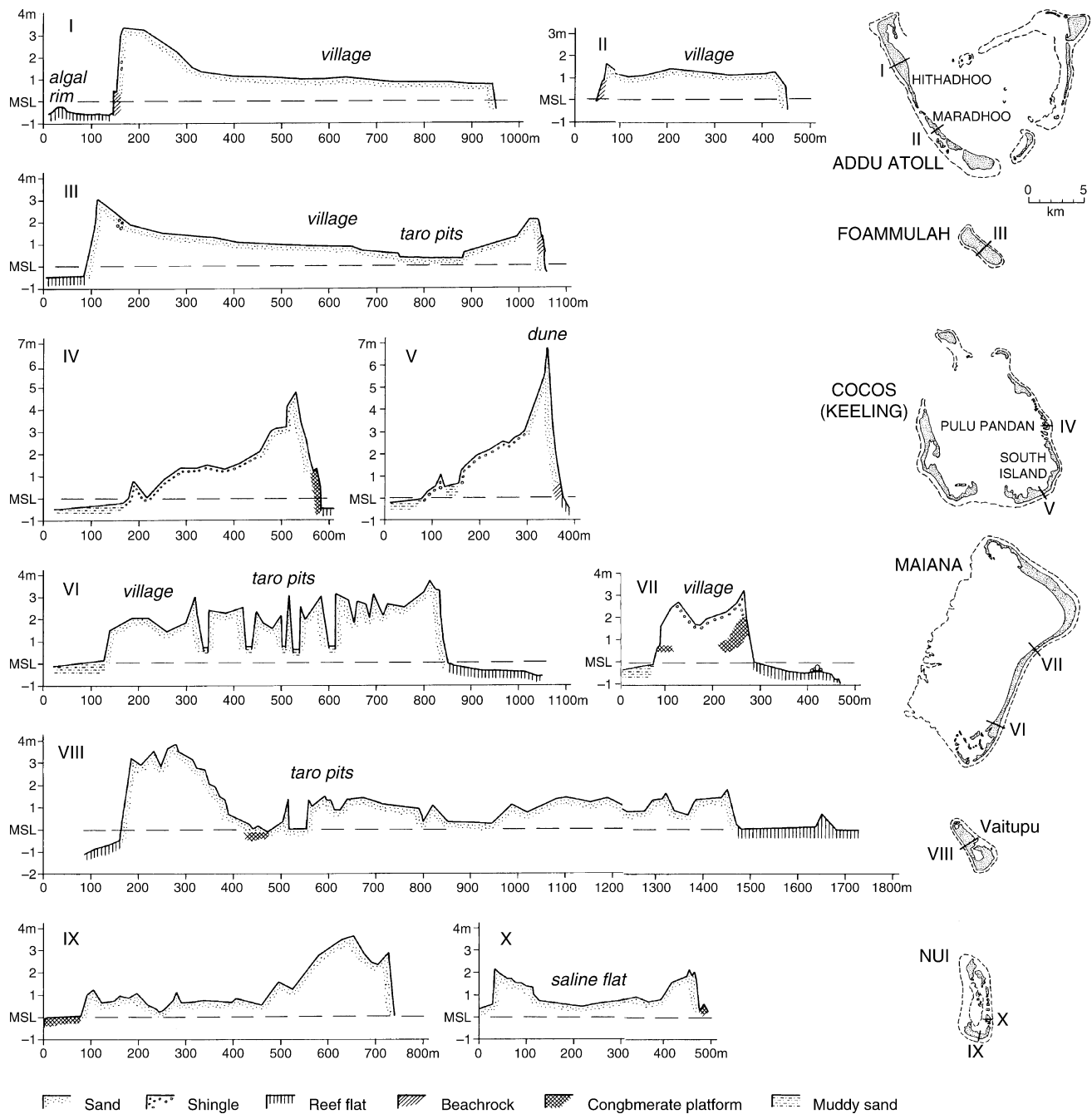
accurate reconstructions of former sea level have been derived where a fossil sea-level indicator can be related to its modern equivalent (see *Sea-Level Indicators*), and the two most appropriate types of indicator are microatolls of massive coral and reef flat outcrops of *Heliopora*.

Outcrops of conglomerate have been used to infer higher sea level in the Maldives (Gardiner, 1903; Sewell, 1936), but the evidence is fragmentary. Dated *in situ* coral from Addu Atoll was interpreted to infer that the reef flat had reached modern sea level by around 3000 years BP (Woodroffe, 1993). Two recent subsequent studies have proposed detailed sea-level curves for the Maldives during the Holocene, but differ on whether or not it is possible to identify evidence to support sea level higher than present in mid Holocene (Gischler et al., 2008; Kench et al., 2009). Based on detailed mapping of conglomerate around Cocos, several *in situ* microatolls have been radiocarbon dated and indicate that there has been a gradual fall of sea level from an elevation 0.5–0.8 m above present over the past 3000 years (Woodroffe et al., 1990b; Woodroffe, 2005).

In the case of islands in the Pacific Ocean there has been a similar debate. The radiocarbon ages reported by Schofield (1977a) from Kiribati and Tuvalu appear to be from corals from the conglomerate that were not in their growth position. The conglomerate in the northern part of the Gilbert chain is composed of a lower unit that contains *Heliopora* in its growth orientation at a few localized sites (Falkland and Woodroffe, 1997; Woodroffe and Morrison, 2001), overlain by an upper unit of disoriented cemented coral clasts. There have been several attempts to infer sea level either geographically (Grossman et al., 1998) or at a site (e.g., French Polynesia, Pirazzoli et al., 1987; Pirazzoli and Montaggioni, 1986, 1988; Funafuti, Dickinson, 1999), but these have not discriminated the *in situ* corals from the more extensive larger conglomerate outcrops. Large sea-level oscillations or abrupt changes appear unlikely, and studies that identify large anomalous fluctuations of sea level have generally been rebutted. For example, evidence for an abrupt fall of sea level around 1300 AD inferred by Nunn (1998) has been criticized by Gehrels (2001) both on the basis of how dating evidence was handled as well as because evidence from a wide geographical area is brought together without regard to spatial variability.

### Reef islands on atolls

A generalized cross-section of an atoll reef island suggests a typical cross-island morphology comprising a distinct oceanward ridge and a lesser lagoonward ridge, with a pronounced swale in the middle. Figure 6 demonstrates considerable variation in reef island morphology, as well as human modification. Waves represent the principal processes that build islands. Open ocean swell is filtered at the reef crest, but a component of the wave energy crosses the reef flat and reaches the island shore. As a consequence,



**Atolls, Figure 6** Reef island cross sections surveyed across a selection of atolls and illustrating the variability in surface topography. Several of the reef islands have been modified through the excavation of pits for cultivation of taro.

reef islands are low-lying; on many Pacific atolls, and also on the Cocos (Keeling) Islands, only about 33% of the reef island surface is more than 2 m above mean sea level, and <8% exceeds 3 m above mean sea level. In the Maldives the islands appear even lower, with around 4 and 1% of the total island area above 2 and 3 m above mean sea level, respectively (Woodroffe, 2008).

#### Island sediments

Atoll reef islands are built from sediments that are entirely calcareous, being derived from the skeletal fragments of organisms living on the reefs, such as coral, coralline or calcifying algae, molluscs, and foraminifera. Genera of benthic foraminifera, such as *Calcarina*, *Amphistegina* and *Baculogypsina*, produced on the reef crest and the reef

flat close to the crest, are a major contributor to the sands from which the islands are composed in Kiribati, Tuvalu, and the Marshall Islands (Woodroffe and Morrison, 2001; Collen and Garton, 2004; Fujita et al., 2009). Elsewhere islands may be composed of coarser material, including coral rubble and shingle. Islands composed of coarser material are often referred to by the Polynesian term *motu* (*Atoll Islands (Motu)*) and differentiated from sandy islands that are called cays (Stoddart and Steers, 1977).

Prominent on many atolls is a conglomerate of disoriented coral blocks, often forming a platform that represents highly resistant substrate where it occurs. Many reef islands appear to be anchored on such outcrops of conglomerate (Montaggioni and Pirazzoli, 1984). Although disoriented coral boulders and cobbles give the conglomerate an irregular appearance, the upper surface is often relatively horizontal, and internal structure may contain distinct beds of various thicknesses. The conglomerates are cemented by coralline algae and marine cements such as isopachous rims of fibrous aragonite or high-magnesian calcite.

Less well-lithified outcrops around the margins of islands include beachrock, which is cemented beach sand, preserving the dip of the original beach. The sands appear to have been cemented beneath the water table, and beachrock may be preserved where sand has been eroded away, indicating former shoreline positions. Cay sandstone is a less well-cemented limestone; this poorly lithified carbonate is horizontally bedded and seems to form associated with the water table within the island interior. On a few islands, the droppings of nesting seabirds have infiltrated into sands in the island interior and they are cemented with a phosphatic cement (Rodgers, 1989). Island surfaces can also be colonized by vegetation, which contributes both directly through roots that stabilize sand and humus that gives the soil greater structure.

Morphological differences have been identified between atolls in storm-prone areas, and those closer to the equator where tropical cyclones (typhoons, hurricanes) are not experienced. Where storms are frequent, reef flats contain abundant coral rubble and large blocks of reef limestone called reef blocks (Bayliss-Smith, 1988). For example, megablocks (*Megablocks*) up to 4 m high and 10 m long were reported to have been deposited on the reef flat of Nukutipipi Atoll in the Duke of Gloucester group in the Tuamotu Archipelago, by the cyclones Veena and Orama that occurred in 1983 (Salvat and Salvat, 1992). Significant impacts were observed after a storm on Jaluit (Blumenstock, 1961). Under some circumstances it appears that tsunamis may detach and emplace large blocks of similar dimensions on coral reefs (Bourrouilh-Le Jan, 1998), but as a tsunami has only a small amplitude in mid ocean, the prevailing view is that these megablocks are emplaced by cyclones. Rubble ramparts are often formed by individual storms (Scoffin, 1993); for example the “Bebe” bank on Funafuti (Maragos et al., 1973; Baines et al., 1974). This rampart has been gradually reworked shoreward across

the reef flat, since it was thrown up during Cyclone Bebe, and in places it has accreted onto similar, but earlier storm-derived deposits on the reef islands (Baines and McLean, 1976). Where storms are less frequent, boulders may accumulate and contribute to a conglomerate that underpins the island. In those atolls closest to the equator and outside the storm belt, such as the Maldives, the islands are predominantly built of sand. Boulder ramparts (*Boulder Zone/Ramparts*) and shingle ridges (*Shingle Ridges*) are indicators of former storm events, and may be eroded and only partially preserved (Pirazzoli, 1987). Rubble storm ridges, deposited over the past 3000 years, are prominent features on islands in Lakshadweep (formerly the Laccadives) to the north of the Maldives (Siddique, 1980).

### Processes of island formation

Almost all material which comprises reefs islands is amenable to radiocarbon dating, and a series of models of reef-island formation on atolls was proposed by Woodroffe et al. (1999). Radiocarbon ages yield estimates of the time of death of skeletal organisms, and deposition may occur some time later, after an undefined period of transport, breakdown, erosion, and redeposition. However, a pattern of gradual oceanward accretion of reef islands appears to have occurred on an elongate island (West Island) on Cocos (Woodroffe et al., 1999), and on Makin at the northern end of the Gilbert chain in Kiribati (Woodroffe and Morrison, 2001). These, and results from comparison of multitemporal aerial photography or satellite imagery (Webb, 2006), indicate ongoing accretion, where sediment production and transport are sustained, on many of the oceanward shores of atoll islands. In other settings there may be more complex trends in shoreline erosion and deposition (Richmond, 1992). For example, detailed resurveys of beaches on the islands of Betio and Buariki in South Tarawa indicate fluctuations of island outline that correspond with wind changes associated with the El Niño-Southern Oscillation phenomenon (Gillie, 1993; Solomon and Forbes, 1999), and in the Maldives seasonal adjustments follow reversal of the monsoon (Kench et al., 2006). An alternative model of island build-up has been proposed for the small sandy islands that occur on patch reefs in the center of the lagoons on atolls in the northern Maldives (Kench et al., 2005). A further approach to determining island formation has been recently developed with the use of computer modeling (Barry et al., 2007, 2008).

### Island soils, vegetation, and ecosystems

The calcareous sediments that form reef islands on the margin of atolls produce poorly developed and immature soils (Morrison, 1990). Soil characteristics depend primarily on the incorporation of plant matter and the development of a humus layer. An exception is the occurrence of phosphate-rich areas, first identified by Fosberg (1957), but subsequently described in several situations where the vegetation is, or was previously, dominated by the tree *Pisonia grandis*. This tree attracts seabirds



and the phosphate enrichment appears related to bird guano.

In contrast to neighboring high islands, the atolls and low islands of the Indian and Pacific Oceans have a relatively species-poor flora. There is a distinct pantropical group of plants that are dispersed effectively across large distances. Many of these plants are strand plants that have seeds that float and can be easily washed up on the beaches around the margins of atolls. Early descriptions of the vegetation and floristics of atolls were undertaken by Raymond Fosberg (1974, 1992), and a major compilation on the vegetation of the tropical Pacific outlines the principal vegetation associations (Mueller-Dombois and Fosberg, 1998).

Several creepers can occur on the beach, such as *Ipomoea pes-caprae* and *Vigna marina*. A coastal fringe of shrubs develops on those sand cays that are not ephemeral, and a broad belt of *Scaevola taccada* and *Suriana maritima* is frequent, often with *Tournefortia argentea* (*Argusia [Messerschmidia] argentea*), which can grow into a small tree. On the larger islands a peripheral belt of shrubs often grades into a forest with trees such as *Cordia subcordata*, *Calophyllum inophyllum*, *Hernandia peltata*, *Guettarda speciosa*, and *Pisonia grandis*. On many atolls the interior is covered with coconut woodland, but in most cases this has been planted and is maintained because the coconut (*Cocos nucifera*) is important for subsistence and often as the basis of a commercial copra industry. A zonation with increasing maturity of vegetation and soils into the interior of reef islands can be recognized, often representing a temporal succession (see [Coral Cays, Vegetational Succession](#)).

The smaller islands tend to contain the least species, and the relationship between number of plant species and island area, particularly based on a study of the vegetation of Kapingamarangi Atoll (Niering, 1963) provided support for the development of ideas on island biogeography by MacArthur and Wilson (1967). However, it is also apparent that the smallest islands, particularly those less than 100m wide, are too small to support a freshwater lens, and only have a restricted strand flora (Whitehead and Jones, 1969). Although on predominantly sandy reef islands there are more species on the larger islands, two further factors are important. On the remote atoll of Suvarrow in the Cook Islands, it is evident that plants are influenced by the substrate, with extensive stands of *Pemphis acidula* sprawled across outcrops of conglomerate (Woodroffe and Stoddart, 1992). Mangrove habitats are also restricted in extent to those few locations where it is sheltered and there is brackish water. Mangroves may occur around the margins of a lagoon (e.g., on Nui in northern Tuvalu, or in the more enclosed embayments as in Vaitupu, Tuvalu, and can also be found in completely enclosed depressions in the center of table reefs, such as Nanumanga, Tuvalu) (Figure 7). On the islands with settlements there are generally many introduced plants (Woodroffe, 1985), including crops such as breadfruit (*Artocarpus*), pandanus, banana and taro (*Calocasia*,

*Cyrtosperma*) and ornamentals, such as the frangipani (*Plumeria*) (Dawson, 1959). Giant taros provide the traditional staple food and are planted in excavated pits. These pits are dug until ground water level is reached. Taros are planted just above the groundwater level and surrounded by woven coconut fronds or pandanus leaves that provide a retaining wall for the plant compost.

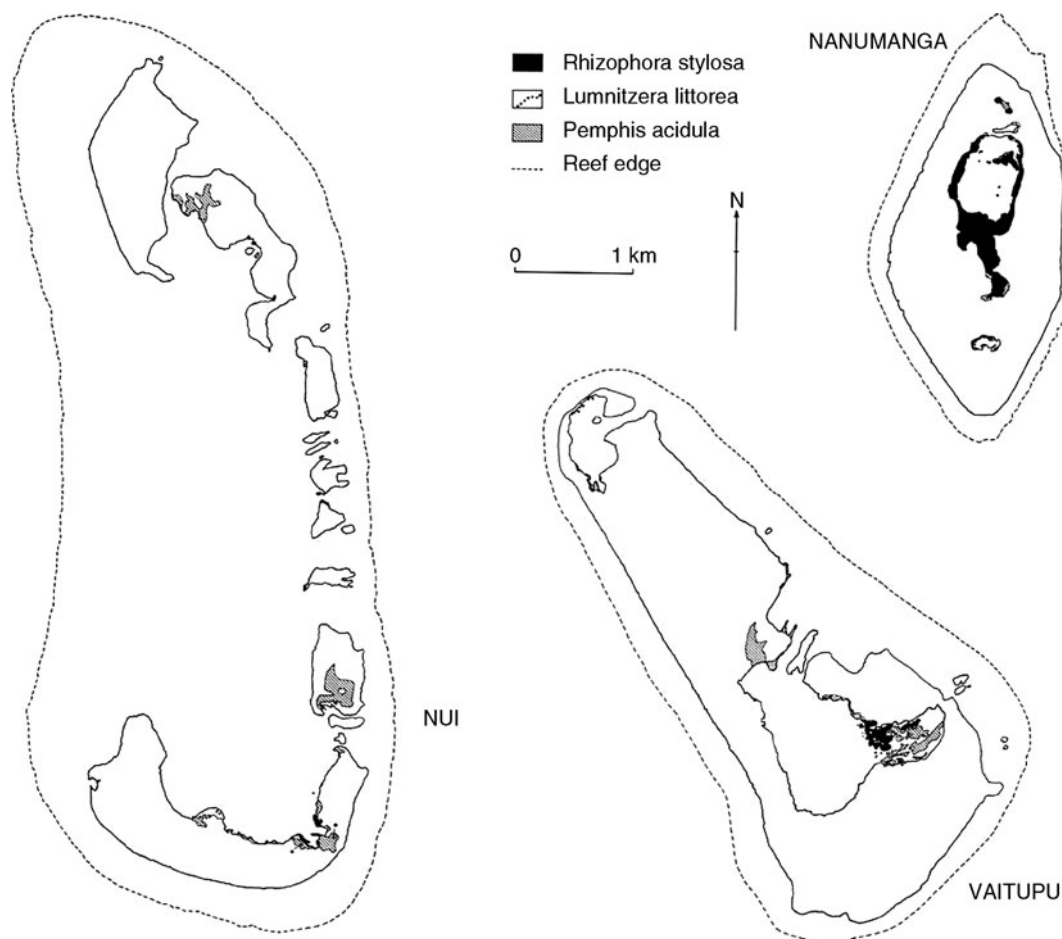
On the most remote atolls, where human visitation is minimal, reef islands can support huge colonies of seabirds. Noddy and sooty terns, boobies, and frigate birds nest in enormous numbers, and if unused to human presence, sit unconcerned while the occasional visitor wanders amongst them. Typically, the ecosystems which develop on atolls are composed of widespread easily dispersed species, and there tends to be a low degree of endemism, presumably because islands have only appeared in the past few millennia on most atolls. Land birds are generally few in number, although there are flightless rails on several atolls. Endemic species are found where the atoll has remained emergent over glacial-interglacial cycles, and not undergone complete submergence during the postglacial sea-level rise. Aldabra in the western Indian Ocean is a noteworthy example with its population of giant tortoises (Arnold, 1976; Stoddart, 1984).

### Atoll hydrology

The small reef islands around the margin of atolls rarely contain freshwater lakes (e.g., Washington in the Line Islands). However, rainwater percolates through the soil and can accumulate as a freshwater lens beneath the island surface. The freshwater lens floats above seawater, and has been characteristically described by the Ghyben-Herzberg principle, that is that the surface elevation of the lens extends above the level of the sea by about 1/40 of the depth to which the lens occurs. The characteristic shape of a Ghyben-Herzberg lens is rarely actually found beneath reef islands because of significant variations in the degree and extent of lithification of the reefal material and in porosity of the limestone (see: [Coral Cays-Geohydrology](#)). A dual aquifer model has been proposed which recognizes the significance of the greater porosity of the Pleistocene limestone that is found beneath the rim of most atolls (Buddemeier and Oberdorfer, 1986). The hydrogeology of several atolls is summarized in reviews by Falkland (1991) and Vacher and Quinn (1997). The elevation of the surface topography influences the water level, and the shape of the lens can also be constrained by well-cemented conglomerate, which may confine the aquifer, as seen in the example of the island of Deke on Pingelap Atoll (Figure 8) in the Marshall Islands (Ayers and Vacher, 1986).

### Human impacts on atolls

The formation of habitable reef islands occurred in mid Holocene, as described above. The history of human occupation therefore is also restricted to the late Holocene, and depends on sea-level history and the accretion of islands



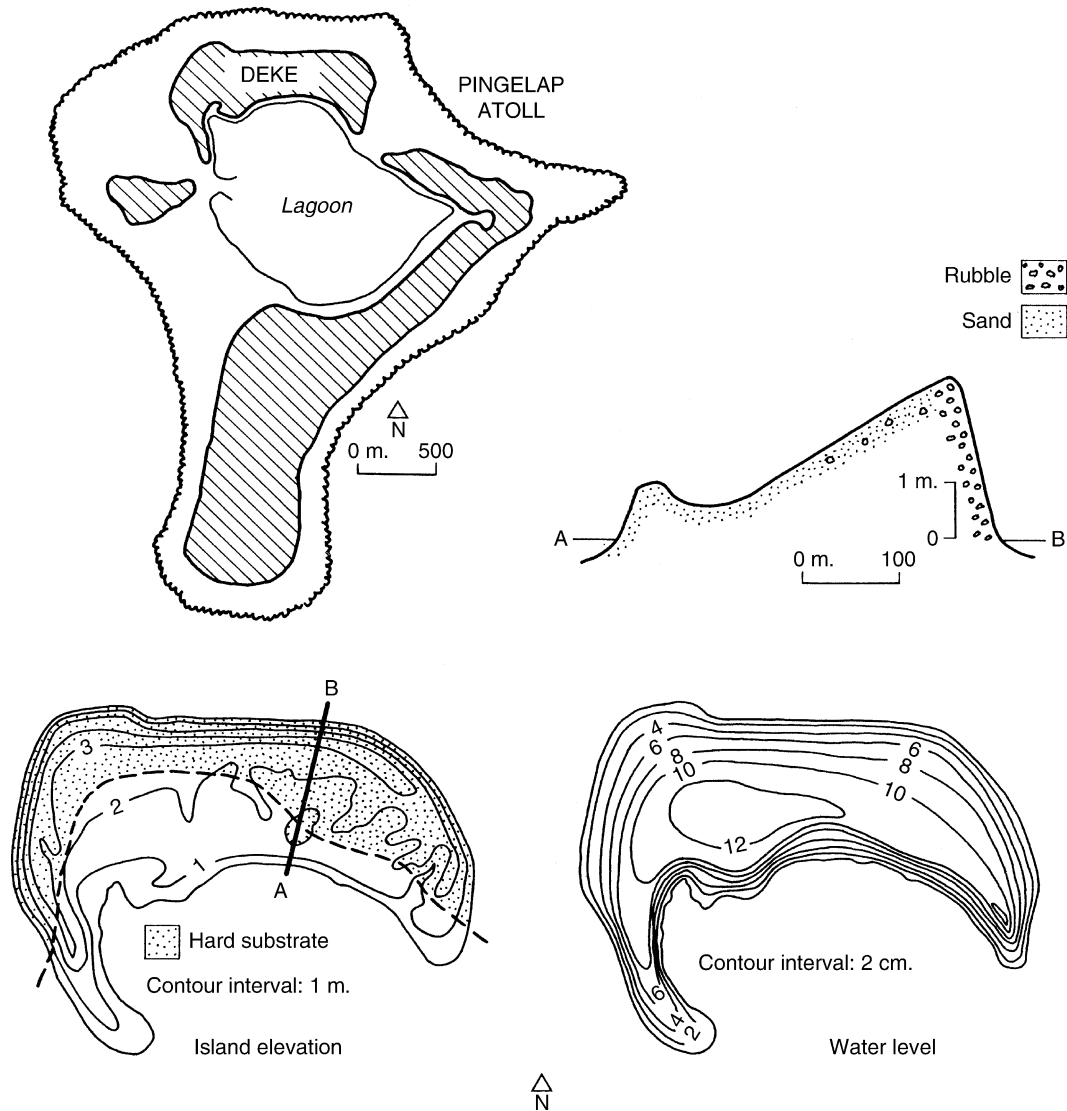
**Atolls, Figure 7** Three atolls in Tuvalu, showing distribution of mangrove and *Pemphis*, and the degree that these environments are impounded (after Woodroffe, 1988).

of suitable size to colonize. In the case of remote atolls in the Pacific, this is often marked by the appearance of *Lapita* pottery (Bellwood, 1987; Weisler, 1994; Nunn, 1999). Human occupation has shaped atoll ecosystems in a number of ways. The vegetation of many has been modified with the planting of coconut plantations, and the introduction of plants as described above.

Human activities have had the greatest impact where there are high population densities (See *Mining and Quarrying of Coral Reefs*; *Engineering on Coral Reefs with Emphasis on Pacific Reefs*). Impacts have affected corals and other carbonate producing organisms. Corals suffer mortality when smothered by sediment (Zann, 1982). Seawater contamination is indicated by increased nutrient levels. Sewerage contains nutrients, and contamination of seawater is often measured by using coliform counts. Increased nutrients can cause localized coral mortality as observed by a high incidence of dead corals on the oceanward reef flat in front of Bikenibeu, a densely populated island on the southern rim of Tarawa Atoll, which has received sewerage outfall in the past (Lovell, 2000).

Domestic waste poses a further threat to ecosystems on some atolls. Certain macrofauna located in the shallow areas of the lagoon at Tarawa may have been organically enriched from land-based anthropogenic sources (Kimmerer and Walsh, 1981; Newell et al., 1996). Also, direct disposal of raw sewerage into the sea has likely increased the seawater nutrient level causing bacterial contamination of the lagoon seawater at Tarawa, but the lagoon ecosystem has been flourishing as a result (Kelly, 1994).

On atolls such as those in the Marshall Islands, Funafuti in Tuvalu and Tarawa in Kiribati increasing population pressure has led to houses being built in inappropriate locations, such as near active beaches and on low-lying areas. In South Tarawa this has prompted the construction of coastal protection structures to avoid overtopping during storms and high water events. There are a large number of reclamations of varying designs and materials built to expand the land area (Figure 9). Betio, Bairiki, and Bikenibeu, the administrative centers of Kiribati, have grown significantly compared to the comparatively pristine islands of Buariki and Abatao on the same atoll,



**Atolls, Figure 8** The atoll of Pingelap, Micronesia, showing a cross-section of Deke Island, and the elevation of the island and the surface elevation of the freshwater lens (after Ayers and Vacher, 1986).

with reclamations and seawalls (both Government and private). Causeway construction between reef islands can have negative physical and biological, as well as social, effects. The position, length, construction method, width of the reefs, and the pattern of water exchange and current strengths mean that causeways can have an influence on both water and sediment transport.

Seawalls pose particular problems. Many are temporary structures built to protect land or expensive assets from erosion. On Tarawa and in the Marshall Islands, they are generally built of coral boulders and beachrock on the margin of land and often extend out onto or across the active beach. Where vertical walls are constructed, these tend to reflect wave energy and can cause scouring

at their base and undercutting (Figure 9). Alternatively, wave overtopping causes infiltration of water leading to structural collapse.

Reclamation and backfilling with sand have provided many people with extra space on small reef islands. Reclamations act like groynes blocking sediment transport along active beaches, with sediment accumulating on the updrift side of structures, while the downdrift side experiences coastal erosion as has occurred on Majuro Atoll (Xue, 2001). Other disturbances to sediment transport pathways can also have severe implications, for example, boat channels, blasted or excavated across the reef flat to provide access for boats at all stages of the tide, also provide conduits for beach sand to be lost over the reef edge.





**Atolls, Figure 9** Human impacts on atoll shorelines, illustrated with examples from Tarawa Atoll, Republic of Kiribati: top left, Oceanside seawall at Nanikai, which reduces access to the ocean; top right, private reclamation; lower left, large reclamation for Mormon Church, Bairiki; lower right, private reclamation that has resulted in erosion of shoreline.

This and similar interventions further disrupt longshore sediment transport, as has occurred on Fongafale, on Funafuti Atoll in Tuvalu (Yamano et al., 2007).

The scarcity of building materials has led to people extracting beach sand and aggregates in large quantities for construction on atolls with a large population. These demands represent a further disruption to the sediment budget causing detrimental impacts such as coastal erosion. On Majuro, chronic erosion has been experienced along lagoonal shores due largely to beach mining (Xue, 2001). Similarly in Vaitupu, Tuvalu, increased sand mining activities in the intertidal zone have reduced beach berm levels, increasing the island's vulnerability to cyclones.

Perhaps the most serious impacts of human activities are yet to be experienced. The impacts of climate change, and in particular sea-level rise, appear particularly ominous for atolls (McLean and Tysban, 2001; Nicholls et al., 2007). There have been several assessments of the vulnerability of atoll reef islands to sea-level rise (e.g., Roy and Connell, 1989, 1991; Lewis, 1989, 1990). Studies of the regional pattern of sea-level rise indicate that the sea is rising with respect to most atolls (Church et al., 2006). The principal

impacts anticipated fall into three categories: shoreline erosion, inundation and flooding, and saline intrusion into the water table (Mimura, 1999). Widespread flooding in the interior of Fongafale on Funafuti Atoll in Tuvalu is often cited as evidence of the effects of sea-level rise, or confirmation that the "islands are sinking" (Pittock, 2005; Patel, 2006). However, Yamano et al. (2007) reconstructed historical conditions showing that the interior of this island was already subject to flooding at the time of the Royal Society expedition in the 1890s. They indicate that construction of an airstrip over former mangrove wetlands further increased the area subject to inundation, and that a considerable degree of human modification, including urbanization, has exacerbated the problem in this instance. Settlement in this densely populated part of the administrative center has encroached on low-lying areas or depressions excavated during military operations (Yamano et al., 2007).

Reef islands are particularly low-lying, although there is considerable geomorphological variability around the margin of any one atoll (Woodroffe, 2008). Islands exhibit a degree of physical resilience, and many may be continuing to build as further sediment is produced through the

growth of calcareous organisms on surrounding reefs and as that sediment is transported onshore. Those parts of atolls that are most resilient, and which can be used sustainably, need to be enhanced by various levels of cultural, or other socioeconomic resilience (Connell, 2003), to reduce the likelihood that atoll communities will collapse in the face of climate or sea-level change (Barnett and Adger, 2003).

## Summary

Atolls represent some of the most remote and lowest-lying land on the planet. Each atoll comprises a reef rim that encloses a lagoon, which may be completed infilled on the smallest table reefs, but can be tens of meters deep on the largest. Lagoons vary considerably in the extent to which they are connected to the surrounding ocean. Carbonate sediment is produced by the growth of reef organisms, and it is swept by oceanic processes, particularly waves, toward the lagoon. On the rims of many atolls, sediment has accumulated as reef islands, which have been colonized first by salt-tolerant plants and in many cases by trees. A freshwater lens underlies the larger islands, and these have attracted human settlements often resulting in coconut plantations and the introduction of other plants and animals. Human impacts threaten the integrity of both terrestrial and marine ecosystems on atolls. Climate change appears likely to exacerbate many of these problems unless a more sustainable approach is adopted to augment the natural resilience of atoll ecosystems.

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## AUVs (ROVs)

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## Synonyms

UUVs, Unmanned underwater vehicles

## Definitions

*AUVs*. Acronym for autonomous underwater vehicles – untethered underwater vehicles under control of an onboard computer.



*ROVs*. Acronym for remotely operated vehicles – tethered underwater vehicles under direct control of a human operator at the surface.

## Introduction

Remotely operated vehicles (ROVs) and autonomous underwater vehicles (AUVs) are increasingly used in studies of deep and shallow coral reefs. As a general rule, AUVs are computer-controlled taxicabs for sensors, need to continuously maintain some degree of horizontal motion, and do not collect physical samples. ROVs are swimming video cameras under direct human control that can stop and hover, and bring back an object or water sample to the surface using a manipulator arm or other mechanical device. However, hybrid AUV/ROVs with combined attributes now exist for military and geophysical surveys (e.g., Saab Double Eagle Seaeye <http://www.seaeye.com/doubleeagle.html>) and deep ocean oceanography (e.g., WHOI Nereus, which reached the Challenger Deep, Marianas Trench in June 2009, <http://www.whoi.com/page.do?pid=10076>). Hybrid AUV designs are particularly well-suited for the demanding navigational environment of coral reef environments because of their increased maneuverability (Dunbabin et al., 2004).

AUVs and ROVs allow the collection of data that might not be otherwise obtainable (Dickey et al., 2008), or at a reduced risk, or cost, compared to other sampling methods such as a scuba diver, towed platform, or ship (Patterson and Relles, 2008). ROVs were initially developed by the defense and oil industries. Maturation of the technology coupled with decreases in vehicle cost led to their adoption as a viable research tool by marine scientists (Stewart and Auster, 1989). In the 1990s, the US National Oceanic and Atmospheric Administration (NOAA) began offering ROV access to scientists funded through its National Undersea Research Program (<http://explore.noaa.gov/>). AUV technology had an intense research and development phase during the 1990s funded largely by national defense agencies (Curtin et al., 1993; Kunzig, 1996), with commercial vehicles not widely available until around 2000. NOAA added AUV access beginning in 2005 (<http://uncw.edu/nurc/auv/glider/pressreleases.htm>). During the past decade, many academic and government institutions purchased commercial AUVs, or transitioned their in-house engineering development AUVs to working research platforms.

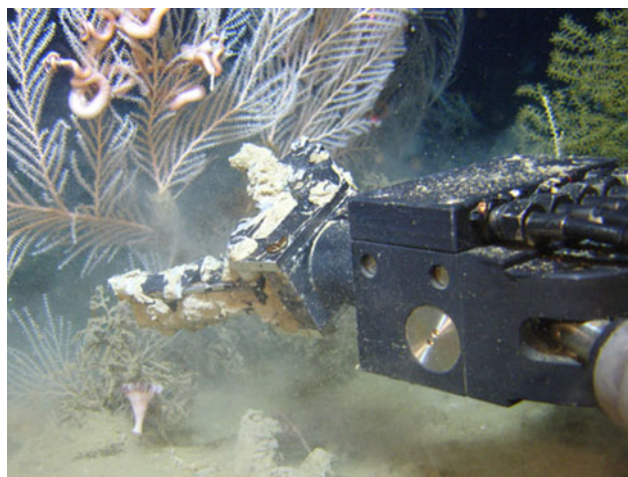
## ROV technology

ROVs range in mass from a few kilograms to several tons, with tethers a few hundred meters to full-ocean depth in length. All ROVs possess a video camera or high-frequency imaging sonar to allow the surface operator to drive the vehicle by visual feedback from the image transmitted over the tether. Maneuvering is provided by orthogonal thrusters that allow independent control of vertical and horizontal motion, including rotation around the ROV's vertical axis. ROVs are usually weighted to almost

neutral buoyancy, allowing them to hover. Most ROVs are supplied with power through the tether, although deep-water ROVs may carry battery power on the vehicle instead, and use the tether only for image transmission and other data telemetry. An example of an ROV is shown in Figure 1. Almost all ROVs possess a manipulator arm under control of the surface operator that allows for the collection of biological or geological specimens (Figure 2). ROVs with sufficient power and size can carry



**AUVs (ROVs), Figure 1** ROPOS ROV on deck during 2006 expedition to deep-water coral reef, Pacific coast, USA. Note manipulator arm on lower right of ROV frame, and numerous video cameras, light sources, and lasers used to determine field of view and size of objects seen on video. Credit: NOAA, <http://oceanexplorer.noaa.gov/explorations/06olympic/logs/may26/media/checking.html>.



**AUVs (ROVs), Figure 2** Manipulator arm on Falcon ROV collecting some alcyonarians/octocorals at a *Lophelia* reef in the Gulf of Mexico in 2008. Credit: NOAA, [http://oceanexplorer.noaa.gov/explorations/08lophelia/logs/sept29/media/falcon\\_rov\\_arm.html](http://oceanexplorer.noaa.gov/explorations/08lophelia/logs/sept29/media/falcon_rov_arm.html).

other payloads including conductivity, temperature, and depth (CTD), acoustic Doppler current profilers (ADCPs), sidescan and multibeam sonars, and more specialized payloads like plankton samplers (Kirkwood, 1998) and micro-electrodes for porewater studies (Luther et al., 1999).

ROVs are most often deployed from a surface ship, and operated a short lateral distance away from the ship. Deep-water deployments may require the surface ship to station-keep using dynamic positioning. Because tether management is a complex task, ROVs are best suited for exploring relatively small (hundreds of square meters), targeted areas of the seafloor, rather than conducting large-area surveys. Geopositioning of the ROV is provided by acoustic means (UltraShort BaseLine – USBL, or Short BaseLine – SBL) relative to the surface ship's position.

### AUV technology

AUVs are free-swimming robots that can gather data with enough spatial and/or temporal resolution to reduce data aliasing (ORION, 2004). Most are torpedo shaped to reduce drag, contrasted with the box-like shape of ROVs, where drag minimization makes little sense given the already high drag of the ROV's tether. AUVs range in length from 1.5 to 5.5 m, with weight in air 20–1,400 kg. AUVs are slightly positively buoyant or have drop weights to produce positive buoyancy at the end of the mission. This ensures the AUV will surface even if onboard control systems have failed. AUVs are battery powered; small AUVs can deploy for several hours, while large vehicles can swim for several days. Survey speeds are usually 1–2 m/s, chosen to maximize range for the onboard battery power. Depth ranges are comparable to ROVs, with many vehicles capable of surveying to continental shelf depths, with few capable of full-ocean depth.

AUVs are well suited to *Swathe Mapping* and large-area surveys. AUVs carry multiple payloads, allowing synoptic coverage; for example, an AUV may simultaneously image the seafloor while measuring water quality. In addition to the payloads listed above for ROVs, AUVs routinely carry fluorimeters, turbidity and turbulence sensors, magnetometers, and water quality sensors

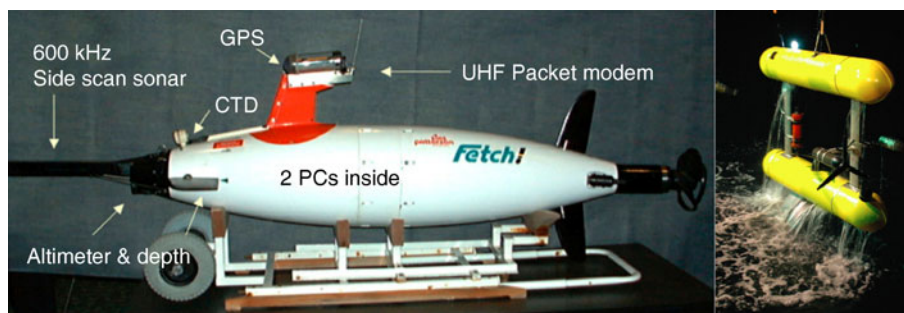
(Hayes et al., 2007; Nicholson and Healey, 2008). AUV position underwater can be determined using acoustic positioning relative to a surface vessel or subsea transponders, or by dead reckoning using a Doppler velocity log to measure speed over the bottom and direction using a compass, or by inertial navigation whereby the accelerations and rotations of the AUV are measured and equations of motion solved. Some AUVs may blend information from several navigational methods to obtain the highest possible accuracy using a nonlinear predictor–corrector algorithm called a Kalman filter (overview of AUV navigation available at <http://www.ise.bc.ca/WADenavandpos.html>).

AUVs are either driven by a propeller (Figure 3), or in the case of gliders, through changes in buoyancy that generate lift on wings on the glider, allowing lateral movement through the water. Propeller-driven AUVs are favored for near-bottom surveys (Patterson et al., 2008); gliders are typically used offshore to investigate currents, water column productivity, or water mass structure (Perry et al., 2008).

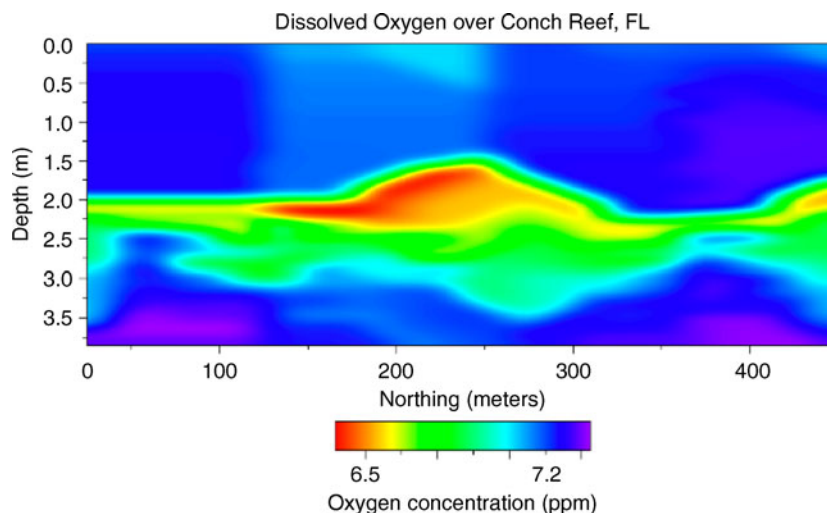
Unlike ROVs, AUVs fly preprogrammed missions, often “mowing the lawn” to survey the seafloor or “yo-yoing” over a reef to measure water quality. However, the flight path can be dynamically altered by the AUV, to adaptively sample features of interest (Fiorelli et al., 2004). Communication with the AUV during the mission can occur via acoustic modem when submerged or via radio frequency (cell phone, WiFi, satellite) when the vehicle surfaces.

### Applications to coral reef science

ROVs have proved very useful in the investigation of deep sea/cold water reefs (*Cold-Water Coral Reefs*) dominated by *Lophelia* (Fosså et al., 2005) and bioherms (*Bioherms and Biostromes*) constructed by *Oculina* (Reed et al., 2005), with video inspections and subsequent specimen collections often discovering new species. ROVs have also provided observational evidence of fish abundance (Parrish, 2006; Stevenson et al., 2007) and invasive species distribution (Kahng and Grigg, 2005) on tropical coral reefs.



**AUVs (ROVs), Figure 3** Examples of AUVs that have surveyed coral reefs. (Left) Fetch1 AUV (Patterson and Sias, 1998; US Patent 5995882), Virginia Institute of Marine Science (VIMS). Credit: NOAA. (Right) Seabed AUV (Singh et al., 2004). Credit: NOAA.



**AUVs (ROVs), Figure 4** Dissolved oxygen mapped over a coral reef in *Florida Keys*, by the Fetch1 AUV, useful in the inference of *metabolism*, *calcification*, and *carbon production*. The unaliased data collected to produce this image could not have occurred without the fast temporal and spatial sampling provided by the AUV. Credit: VIMS.

AUVs have mapped currents and bathymetry of coral reefs over large areas in deep water (Grasmueck et al., 2006), and made detailed photomosaics in shallower water (Armstrong et al., 2006). The physical oceanography of tropical coral reefs has also been surveyed by AUVs, including currents (Fong and Jones, 2006), plume dispersion (Jones et al., 2008), and hydrography and bathymetry (Shcherbina et al., 2008). AUVs are also well-suited to collect water quality data (Figure 4). Because AUVs can move sensors rapidly over a reef, they can help address the problem of data aliasing; aliasing occurs when data are sampled too coarsely in space or time to provide an understanding of nature's dynamics.

ROVs and AUVs are well suited for collecting video and still imagery, allowing analysis of landscape level patterns on reefs through photomosaic construction (Lirman et al., 2007; Ludvigsen et al., 2007). Mosaics of photos, side scan sonar, and multibeam sonar gathered by AUV or ROV are managed in a *Geographical Information System (GIS)*, providing reef scientists a useful tool for environmental monitoring, including assessment of the efficacy of marine protected areas (Patterson and Relles, 2008).

## Summary

Underwater robots such as AUVs and ROVs can gather data from reef systems over depth ranges, and at time and frequency scales, that cannot be obtained easily using other sampling techniques. Both technologies can serve as taxicabs for sensors and imaging systems, with AUVs well suited for large-area surveys, and ROVs suited for sample retrieval and video inspection of more limited areas.

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## Cross-references

Bahamas  
 Cold-Water Coral Reefs  
 Florida Keys  
 Patch Reefs: Lidar Morphometric Analysis  
 Reef Front Wave Energy  
 Remote Sensing  
 Seagrasses  
 Swathe Mapping  
 Waves and Wave-Driven Currents  
 Western Atlantic/Caribbean, Coral Reefs



# B

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## BACK-STEPPING

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### Synonyms

Transgressive reef

### Definition

Shallow-reef systems back-step to keep up with rapid relative sea-level rise. Back-stepping involves the demise of shallow-reef development at one site, and its relocation to another site further inshore and up-shelf. It is common during the onlap or retrogradation of tropical carbonate systems in transgressive systems tracts, and typical of glacial terminations during the Quaternary Ice Age.

### Introduction

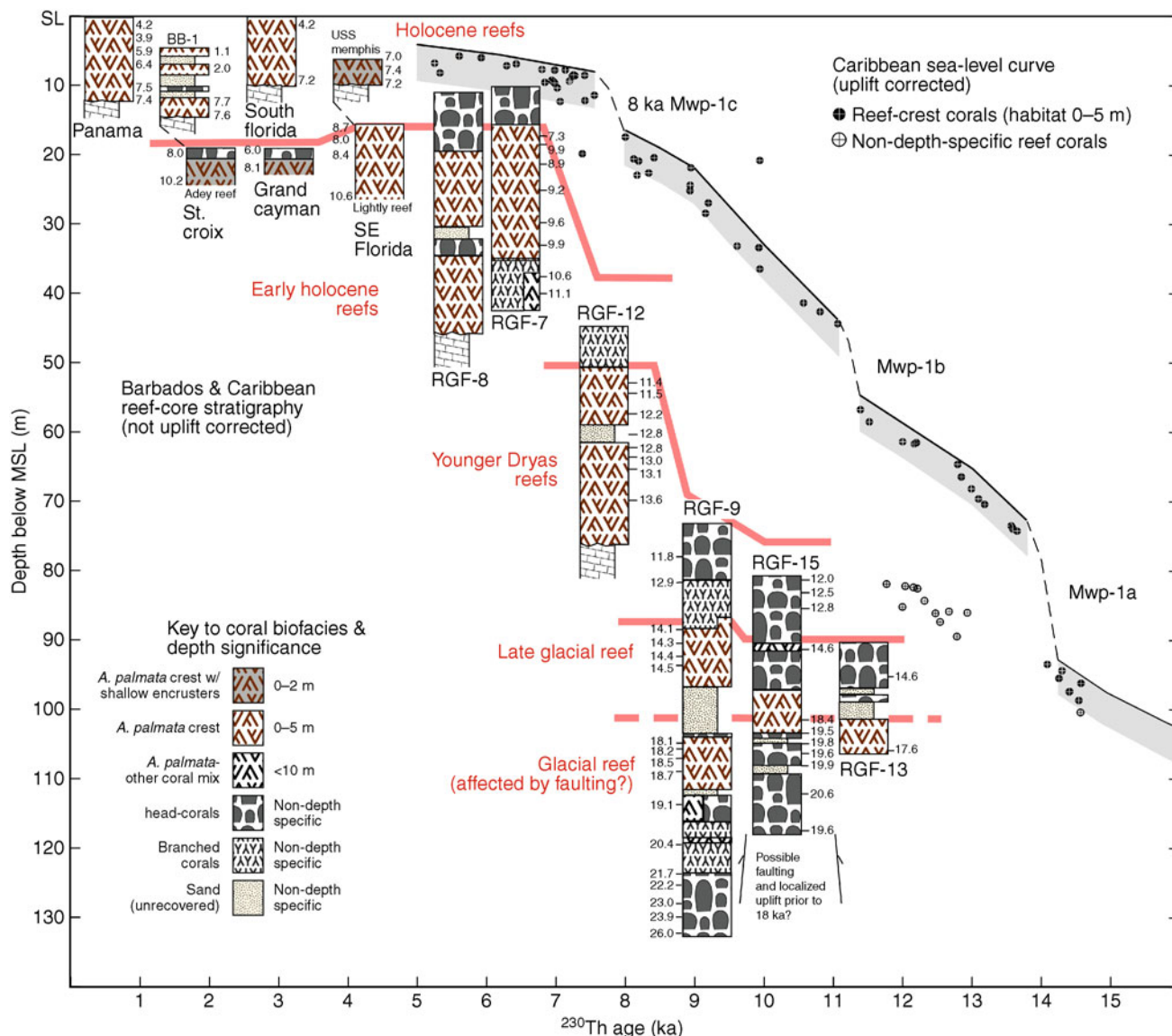
Reef back-stepping has been widely recognized from the geological record where it is almost universally interpreted as a result of rapid rise in relative sea level (Smith and Stearn 1987; Kaufman and Meyers 1988; Ross 1992; Becker et al., 1993; Wendte and Uyeno 2005). Yet ironically, there has been considerable argument over its existence and significance in late Pleistocene and Holocene reefs. This largely stems from early assumptions that healthy reefs could accrete faster than the average rate of glacio-eustatic sea-level rise (Adey et al., 1978; Schlager 1981). Reef drowning in the strictest sense was therefore considered uncommon and only ‘incipient drowning’, where shallow reefs were initially submerged but subsequently recovered when the rise rate declined, was considered likely (Kendall and Schlager 1981). According to this early view, complete drowning of healthy reefs by

submerging them below the euphotic zone (~100 m) required exceptional circumstances: either a combination of regional subsidence and pulsed sea-level rise which removed the reef from the low-stand euphotic zone, or more local environmental factors to suppress the accretion potential of reefs and make them susceptible to drowning (Adey 1978; Kinsey and Davies 1979; Neumann and Macintyre 1985; Hallock and Schlager 1986; Vogt 1989; Hubbard et al., 1997).

Given the impact of global environmental deterioration on modern reefs, particularly those resulting from greenhouse gas emissions, it is important to clarify arguments concerning the cause of reef demise and back-stepping. This is because the processes postulated to have caused reef demise and back-stepping in the past are very similar to ones that have been identified as threatening reefs in the future. In this light, the investigation of reef back-stepping in the recent past is taking on a new sense of urgency.

### Reef back-stepping in stable terranes

The discovery of back-stepping in Quaternary reefs occurred when Fairbanks (1989) drilled submerged, postglacial reef terraces off the south coast of Barbados. His cores showed three back-stepping reefs containing thick monospecific sequences of the reef-crest coral *Acropora palmata*, which has a depth-restricted habitat range of ~5 m (Figure 1). By dating this reef-crest coral, he identified two rapid rises in postglacial sea level termed meltwater pulse (Mwp) 1a and 1b, but never analyzed the stratigraphy or recognized the significance of reef back-stepping *per se*. That recognition was made by Blanchon and Shaw (1995), who used elevation differences between the *A. palmata* sequences, and their transition into succeeding units, to constrain the rate and magnitude of those rapid-rise events. By including evidence from other submerged reef crests in the Caribbean, they also identified a rapid rise (Mwp-1c) in the early Holocene which caused a third reef back-stepping

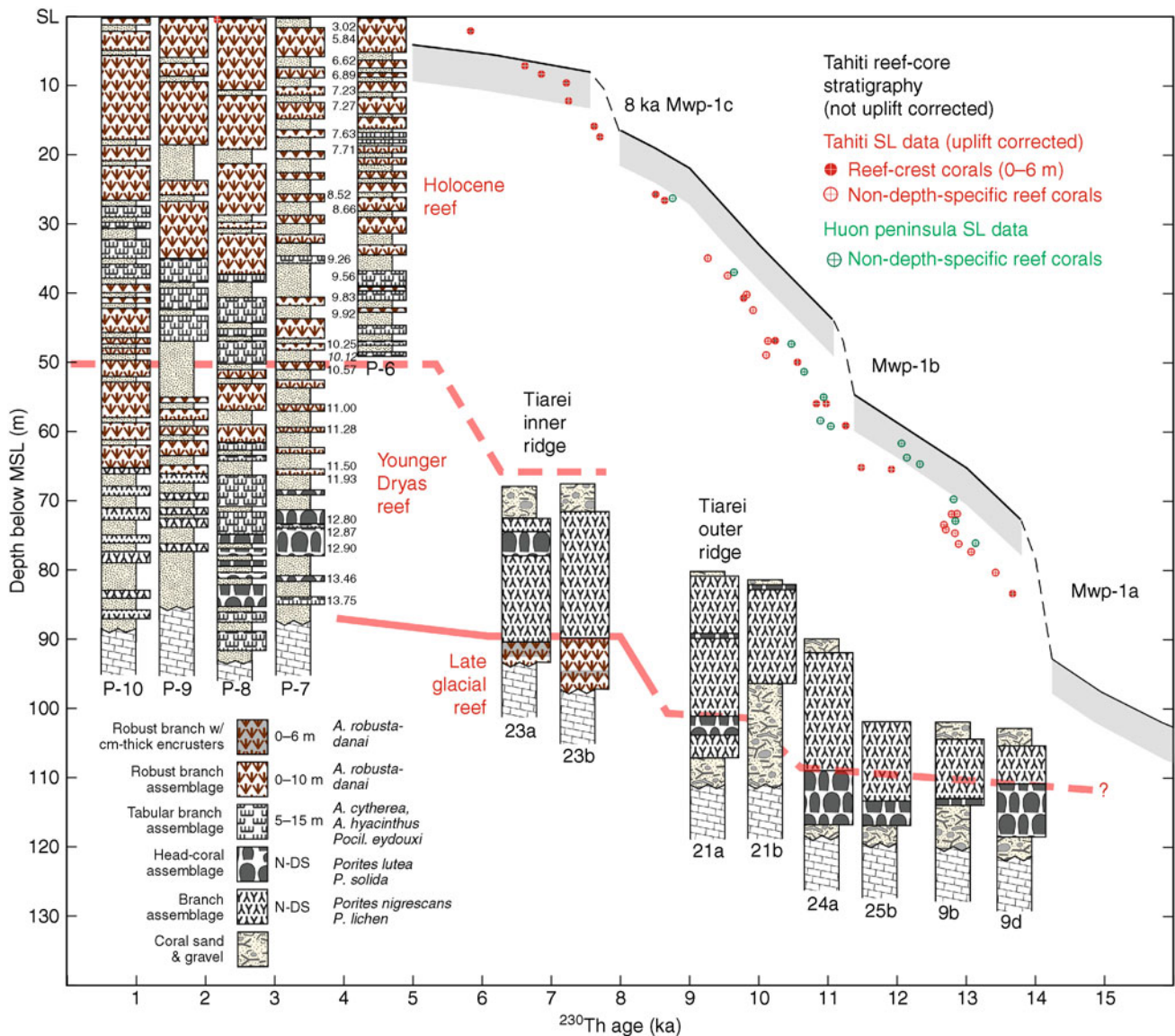


**Back-Stepping, Figure 1** Caribbean three-step model of postglacial sea-level rise and the back-stepping reef-core stratigraphy. Reconstruction of sea level older than 8 ka uses uplift-corrected elevation and thickness of back-stepping *A. palmata* reef-crest sequences from Barbados, and precise  $^{230}\text{Th}$  ages from corals in those sequences (Fairbanks 1989; Blanchon and Shaw 1995; Peltier and Fairbanks 2006). Reconstruction of sea level younger than 8 ka is from back-stepping stratigraphy and calibrated radiocarbon-ages of relict and active Holocene reefs in tectonically stable areas of the Caribbean (Blanchon et al., 2002; Toscano and Macintyre 2003). The position of mean sea level is identified from coral age/elevation data that falls within a 5 m envelope (shaded), which represents the 0–5 m reef-crest habitat depth zone where *A. palmata* forms a monospecific assemblage mixed with clasts. Outliers from this envelope are a result of either upslope transport during storms, or from deeper habitat ranges of non reef-crest corals. Correction for continuous uplift of Barbados is assumed to be 0.34 mm/year but is ignored in order to quantify the rate and magnitude of sea-level jumps that caused episodes of reef-crest drowning and back-stepping.

event that led to the establishment of modern Caribbean reefs (Blanchon et al., 2002).

The discovery of reef back-stepping and rapid sea-level jumps in the Caribbean led others to look for similar events in other regions. Two cores recovered from the reef crest around Tahiti by Bard et al., (1996) found that the modern reef initiated there immediately following

Mwp-1a, much earlier than in the Caribbean, and then kept pace with sea-level rise (Figure 2). The lack of evidence of reef back-stepping during Mwp-1b and 1c led Montaggioni et al., (1997) to question the magnitude and/or existence of these events. However, the keep-up interpretation of the Tahiti cores was contested by Blanchon (1998) who argued that Indo-Pacific reefs might



**Back-Stepping, Figure 2** Tahitian reef-core stratigraphy and age-elevation data, compared to the Caribbean postglacial sea-level curve. Core stratigraphy shows a single episode of reef-crest back-stepping following Mwp-1a (P-core stratigraphy from Montaggioni et al. [1997] and Cabioch et al. [1999], ages from Bard et al. [1996]; Tiarei cores interpreted from data in Camoin et al. [2007]). Note that facies sequence in the late-Glacial cores from the Tiarei inner-ridge shows a biofacies inversion from robust-branching corals typical of high-energy environments to delicate-branching corals typical of low-energy settings. This inversion is typical of recolonization of drowned reefs by deeper-water coral assemblages. Tahitian and Huon Peninsula age-elevation data generally plots below Caribbean curve but shows a distinct pattern related to meltwater pulses 1a and 1b. The magnitude of the offset is largest following meltwater pulse events and gradually decreases thereafter. This pattern is consistent with submergence of Tahitian and Huon reefs of following sea-level jumps and gradual catch-up of the reef-surface with sea level. For the first two meltwater pulses, it can be seen that the offset is  $>10$  m and coincides with a change of biofacies. The offset related to the 8 ka jump however is  $<10$  m and coincides with a minor biofacies change in only one core, P6.

be relatively insensitive to rapid sea-level jumps because their assemblage of reef-crest corals had a larger depth range (10 m) and were more diverse and difficult to identify in core. This is supported by quantitative analyses of coral assemblages on the adjacent island of Moorea by Bouchon (1985) who found that the shallow crest assemblage of robust-branching corals extended down

the reef-front slope to  $\sim 10$  m. As a result, Blanchon (1998) suggested that back-stepping may not have been recorded because the magnitude of sea-level jumps during Mwp-1b and 1c was not sufficient to displace the Tahitian reef-crest assemblage out of its 10 m habitat zone, and the reefs rapidly rebuilt to sea level without registering a significant facies change in the cores.



Later coring on the Tahitian reef crest, however, showed systematic changes in coral assemblages which corresponded to the timing of Mwp-1b (Cabioch et al., 1999). Following Mwp-1a, the base of the sequence started in lower-reef-front slope assemblages (>10 m) but shallowed into upper-slope assemblages (<10 m) shortly before Mwp-1b. Following that rise event, assemblages reverted to lower slope as waters deepened, but quickly shallowed thereafter, and showed little or no subsequent changes related to Mwp-1c (Figure 2). In other words, the reef crest recovered following the first two meltwater pulses but did not register the last.

Despite the lack of clear facies changes registered at Tahiti during the 8 ka meltwater pulse, further evidence of reef demise and back-stepping has since been reported from several other areas around this time. Off the north coast of St. Croix, Hubbard et al. (2005) recovered core sequences from the interval of modern reef initiation, and found that *A. palmata* reef-crest assemblages had developed at 12 m by 7.7 ka (Figure 1). The comparison of this initiation age, with the terminal age of an early Holocene reef crest off the southwest coast (Adey et al., 1978), shows that reef back-stepping started at ~8 ka at a depth of ~21 m and was complete by 7.7 ka at 12 m. Although the precise age and depth of the early Holocene reef crest are uncertain due to the lack of core coverage, heavy encrustation of the cored *A. palmata* by coralline algae indicates that the reef-crest position could be no shallower than 18 m (cf. Steneck and Adey 1976). In other words, these data indicate St. Croix's reef-crest back-stepped 4–7 m in 300 years or less.

Similar evidence of rapid back-stepping has also recently been confirmed from southeast Florida, where Banks et al., (2007) reported coral ages from a single core and submarine grounding site (USS Memphis in 1993). These data indicate that a reef-crest facies, consisting of in-place *A. palmata*, initiated on the inner shelf 7.4 ka ago at 10 m below sea level (see inner reef-tract in Figure 3). Comparing the initiation age of this shallow reef with the demise of a deeper, early Holocene reef crest exposed in a sewage-outfall trench a further 3 km offshore (Lighty et al., 1978), shows that reef back-stepping had started by ~8 ka at a depth of ~17 m and was complete by 7.4 ka at 10 m (see outer reef-tract in Figure 3). These data therefore indicate that southeast Florida reef crests also back-stepped 4–9 m in ~450 years.

In addition to the Holocene and deglacial events, back-stepping has also been documented during the last interglacial highstand (MIS-5e) when sea level was as much as 6 m higher than present. Along the Red Sea coast of Eritrea, for example, an uplifted and tilted LIG reef sequence near Abdur clearly shows two superimposed stages of shallow-reef development (Bruggemann et al., 2004). The lagoon and patch-reef section of the lower reef unit is truncated by an intermittent marine-erosion surface and directly overlain by a 3 m crest and reef-front section of the upper-reef unit. This implies that reef-crest development back-stepped over an existing reef lagoon. But given the neotectonic

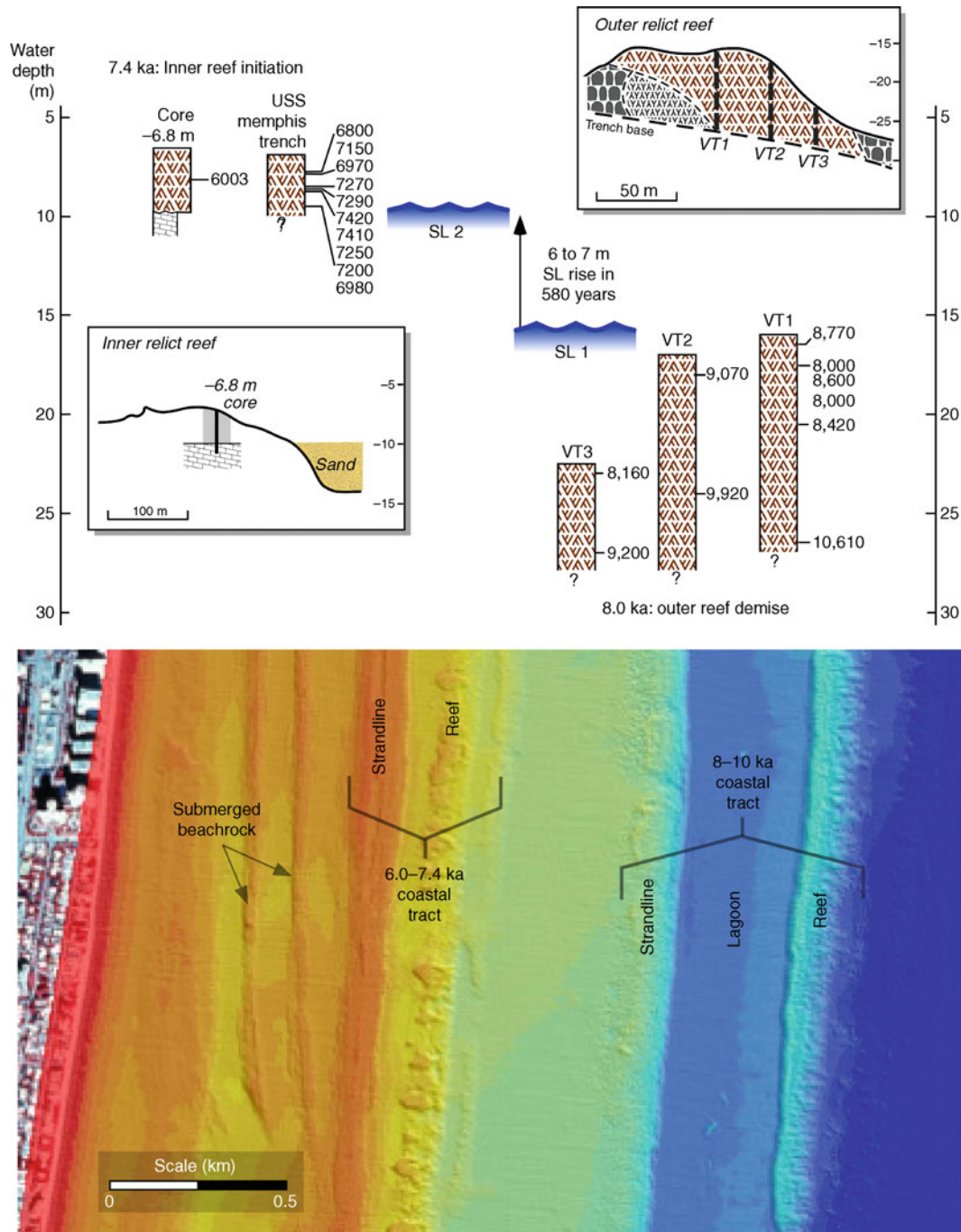
setting of this site, the possibility that co-seismic uplift produced reef back-stepping cannot be discounted.

A clearer example of back-stepping has recently been described from the northeast Yucatan by Blanchon et al., (2009) and Blanchon (2010). Two superimposed fossil reef units were documented. A lower patch-reef complex and adjacent crest unit at +3 m is overlain by a second reef unit with a crest at +6 m. Reliable radiometric ages confirmed both units were of last interglacial age but could not differentiate between them, mainly due to subtle diagenetic alteration of corals in the lower unit. However, the relative-age relations between the two units were clear. The framework of the upper-reef unit was infiltrated by shelly beach-gravel as sea level fell at end of the interglacial, but infiltration of lower reef was prevented by cap of crustose coralline algae. This infiltration pattern shows that the upper reef was younger and must have been alive shortly before sea level fell, and that the lower-reef was older and was dead when sea level fell. Areas of continuous accretion between the lagoonal patch reefs of the lower unit and reef crest and back-reef of the upper unit, however, require that the demise of the lower-reef was ecologically synchronous with initiation of the upper-reef tract. In other words, back-stepping took place on an ecological timescale. The relative differences between the elevations of the reef crests and flats in the two reef units, and the presence of 1.5-m tall colonies at the base of the upper-crest unit, indicate that this back-stepping was a result of a 2–3 m sea-level jump at the end of the last interglacial (Blanchon et al., 2009).

### Reef back-stepping in subsiding terranes

As suggested by Schlager (1981), the combination of subsidence and pulsed glacio-eustatic sea-level rise provides an ideal mechanism to trigger reef back-stepping. A good example has been described from the Huon Gulf, Papua New Guinea, where rapid and oblique convergence of the Australian and West Pacific plates, and intervening microplates, has produced a foreland basin with high rates of vertical displacement across its collisional axis (e.g., 12 mm/year; Abers and McCaffrey 1994). Flexure of the basin's cratonic margin has caused submergence and onlap during the last ~450 kyr and produced as many as 14 back-stepping platforms, with 7 confirmed as reefal in origin but with only 1 returning a reliable radiometric age (Galewsky et al., 1996; Webster et al., 2004a, b). Coral fragments from the base of platform PII recorded an age of ~60 ka, but there was no direct evidence for it being reefal in origin (Webster et al., 2004a). A single age from the talus of platform PXII, that is clearly reefal in origin, indicates that it was likely drowned by a major deglacial sea-level rise associated with the transition from MIS-10 to 9 (Galewsky et al., 1996; Webster et al., 2004b). However, the number of confirmed reefal platforms clearly exceeds the number of major deglaciations, and indicates that interstadial sea-level-rise events may also be responsible for platform drowning (Webster et al., 2009).





**Back-Stepping, Figure 3** Exposures in back-stepping relict breakwater reefs from Southeast Florida, and their implications for the rate and magnitude of Holocene sea-level rise. *Upper inset* shows morphology and facies of the outer relict-reef (Lighty et al., 1978), and below, an age–depth plot of *A. palmata* samples from three vertical transects (VT) shown on inset (calendar age and depth of samples reported by Toscano and Macintyre [2003]). Calendar ages in **bold** show timing of outer relict-reef demise at ~8.0 ka. *Lower inset* shows morphology and facies of the inner relict-reef depth (Banks et al. (2007), and above, an age–depth plot of *A. palmata* samples from a core at –6.8 m and an exposure 8 km further south made during the USS Memphis grounding. Calendar ages in **bold** show that initiation of inner relict-reef was ~7.4 ka. As such, these age–depth data show that reef-crest corals died off 8.0 ka ago and back-stepped 6 m vertically upslope in only 580 years, initiating a new phase of reef-crest development by 7.42 ka. This rapid back-stepping of reef crests could only happen if there was a 6 m jump in Holocene sea level. Below, LiDAR digital depth model showing positions of relict reef and coastal tracts sampled in exposures described in upper figure (Courtesy of Brian Walker and Bernhard Riegl, Nova Southeastern University).

Another good example of reef back-stepping in a rapidly subsiding terrane has been reported from Hawaii (Webster et al., 2004a, 2007). There, average long-term subsidence associated with volcanic loading of the lithosphere has been measured at 2.7 mm/year over the last ~500 kyr (Sharp and Renne 2006). This submergence coupled with glacio-eustatic sea-level change has produced 12 back-stepping linear ridges, of which 3 have been confirmed as reefal in origin and have radiometric ages (H7, 392 kyr; H2, 136 kyr; H1, 14.7 kyr; Webster et al., 2009). The oldest of these ridges (H7) returned U-series ages of 392–377 ka from corals at the base of the sequence. But this sequence also showed evidence of erosional breaks indicating the ridge may, in fact, be a composite unit consisting of several superimposed episodes of reef development (Webster et al., 2009). This preliminary evidence of multicyclic ridge development is also consistent with simulated reef development during the last two glacio-eustatic sea-level cycles (Webster et al., 2007).

The youngest of the Hawaiian ridges (H1) is a composite feature, consisting of three closely-spaced ridges between 150 and 105 m water depth. The deepest ridge has been investigated by ROV and samples from in-situ corals collected from the reef crest, returned ages of 15.8–14.7 kyr indicating that it drowned following Mwp-1a (Webster et al., 2004c). However, it is unknown if these ridges consist of single reefs formed during a single sea-level position or multicyclic sequences formed during more than one sea-level position.

### Cause of reef back-stepping

In both stable and subsiding terranes, the above evidence indicates that the proximate cause of reef drowning and back-stepping is rapid sea-level rise, particularly jumps in sea level caused by pulses in meltwater and iceberg discharge during deglaciation (Blanchon and Shaw 1995; Webster et al., 2004c). Direct measurement of the rise rates during these jumps clearly falsifies early assumptions that reefs can easily outpace sea-level rise, and therefore largely negates the paradox of reef drowning (Schlager 1981). Indeed, sea-level rise rates during these jumps exceed the accretion potential of modern and late Pleistocene reefs by as much as six times.

In addition to the rise rate, however, the magnitude of the jump is also critical for the drowning and back-stepping response of reefs. Evidence indicates that the ~15 m sea-level jump during Mwp-1a produced an ubiquitous back-stepping response from late Glacial reefs at all sites investigated. Cored reef sequences from the oceanic islands of Tahiti and Barbados both show that the position of shallow-reef development switched to an upslope location in 500 years or less. On Barbados, *A. palmata*-dominated crests moved upslope between 11 and 16 m in <450 years (although that duration could be significantly reduced by dating the base of the reef-crest sequence in RGF-12 in Figure 1). Whereas on Tahiti, new drilling on

the fore-reef slopes during IODP-310 has identified drowned reefs related to the back-stepping following Mwp-1a (Camoïn et al., 2007), and indicates that reef relocation started at 14.6 and was complete by at least 14 ka (although the precise timing and magnitude of this back-stepping remains to be reported) (Figure 2). The isolated oceanic nature of these two islands means that this back-stepping event took place in healthy reef systems that were largely unaffected by conditions that could suppress their accretion potential and make them more susceptible to drowning (such as rapid flooding of extensive continental shelves). As a consequence, their back-stepping provides clear support for the singular role of large-magnitude jumps in sea level. It is likely that jumps of this magnitude submerged reefs below an optimal accretion window and re-established this window far enough upslope that the original communities were unable to recover due to rapid deterioration in light levels and/or sediment flux. This is supported by core sequences from both islands, which show an immediate switch to deeper-water communities following Mwp-1a and indicate that only 10–15 m of subsequent deep-reef accretion took place. In the case of Barbados, that accretion had ceased completely by ~12 ka when sea level had submerged the drowned reef by ~30 m (see RGF-15 in Figure 1, but note that accretion in RGF-9 may have been supplemented by downslope sedimentation from early reef growth at RGF-12).

The response of reefs to the subsequent smaller magnitude sea-level jumps, however, was not consistent between oceanic reef provinces. In the Caribbean, for example, Mwp-1b did trigger reef back-stepping. Barbados cores show that a reef-crest sequence at 50 m in RGF-12 was abruptly replaced by a deeper *A. cervicornis* unit, and shifted 5–10 m upslope in <314 years in RGF-8 (Figure 1). But at Tahiti, no evidence of back-stepping has been found in cores through the modern reef crest, where the sequence simply shows a switch from robust-branching to tabular-branching assemblages at ~50 m. It should be noted that this lack of evidence does not mean that back-stepping did not occur, just that it is undocumented. It might be that the islands fringing reefs, which have largely been ignored, initiated at this time.

A similar lack of consistency also resulted from the final sea-level jump, Mwp-1c, starting at 8 ka. In the Caribbean, many areas including Barbados show *A. palmata* reefs that established at the beginning Holocene had died off by ~8 kyr, just as modern reef structures were initiating (Figure 1; Blanchon et al., 2002). Initial explanations of this early Holocene die-off were formulated before there were adequate data on the age of modern reef initiation, and so the close timing between the two generally went unappreciated. Subsequently, however, the age of modern reef initiation has been reported from many areas including, more recently, southeast Florida and St. Croix where it occurred between 7.8 and 7.6 ka at depths of 10–12 m (Figures 1 and 3). Drowned reefs that died off during the 8 ka jump have also been reported from several areas, most recently Grand Caymen and the

Gulf of Carpentaria where their reef crests occurred at a depth of ~20 m (Blanchon et al., 2002; Harris et al., 2008). So, between 8 and 7.6 ka reef-crest sequences throughout the Caribbean, and perhaps other areas, back-stepped upslope between 4 and 8 m (Figure 1 and 3). Yet despite all this activity in the Caribbean and other seas, reef sequences in Tahiti apparently show no evidence of back-stepping at 8 ka, and don't even register a response in the facies sequence (Figure 2).

The key question then is why should Tahitian reefs, and possibly Indo-Pacific reefs in general, be more resilient to rapid sea-level jumps than those in the Caribbean? An obvious possibility is that the greater diversity and depth range of Indo-Pacific reef-crest assemblages provides a broader insurance coverage against the environmental changes wrought by rapid sea-level jumps. In Caribbean reefs, with their shallow and almost monoculture-like crest assemblages, such rapid changes must be difficult to insure against and they therefore have a much greater impact. A clear example of this vulnerability is illustrated by the back-stepping event during the last interglacial from the northeast Yucatan (Blanchon et al., 2009). In this case, even a small 3 m jump led to an unfavorable sedimentation regime that resulted in the severe restriction of reef development along the northeast coast of the Peninsula and apparently to extirpation of reefs in the Bahamas and other low gradient coasts (perhaps even as far a-field as western Australia).

The ongoing widespread decline of Caribbean reefs, however, is perhaps the strongest evidence of this vulnerability. While Indo-Pacific reefs show increasing signs of being resilient to rapid environmental changes (Adjeroud et al., 2009; Diaz-Pulido et al., 2009), coral cover in the Caribbean continues its steep decline (Gardner et al., 2005). The cause of this dramatic degeneration is widely debated, but recent analyses indicate that chronic human disturbance via overfishing and nutrient input, coupled with disease outbreaks, has synergistically impaired the regenerative potential of reefs following major disturbance events, such as hurricanes or thermal mass bleaching induced by global warming (Gardner et al., 2005; Mora 2008; Mumby and Steneck 2008; Raymundo et al., 2009). Add to this the increasingly dire predictions of future rapid sea-level rise, and what we could be witnessing in the Caribbean is the initial stages of the next episode of reef demise and back-stepping.

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## Cross-references

[Last Interglacial and Reef Development](#)  
[Meltwater Pulses](#)

## BAFFLESTONE

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Bafflestone is a modification of Embry and Klovan (1971) to the Dunham (1962) Boundstone limestone type. It recognizes that the framework organisms acted as baffles to sedimentation.

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## Cross-references

[Classification of Carbonates](#)

## BAHAMAS

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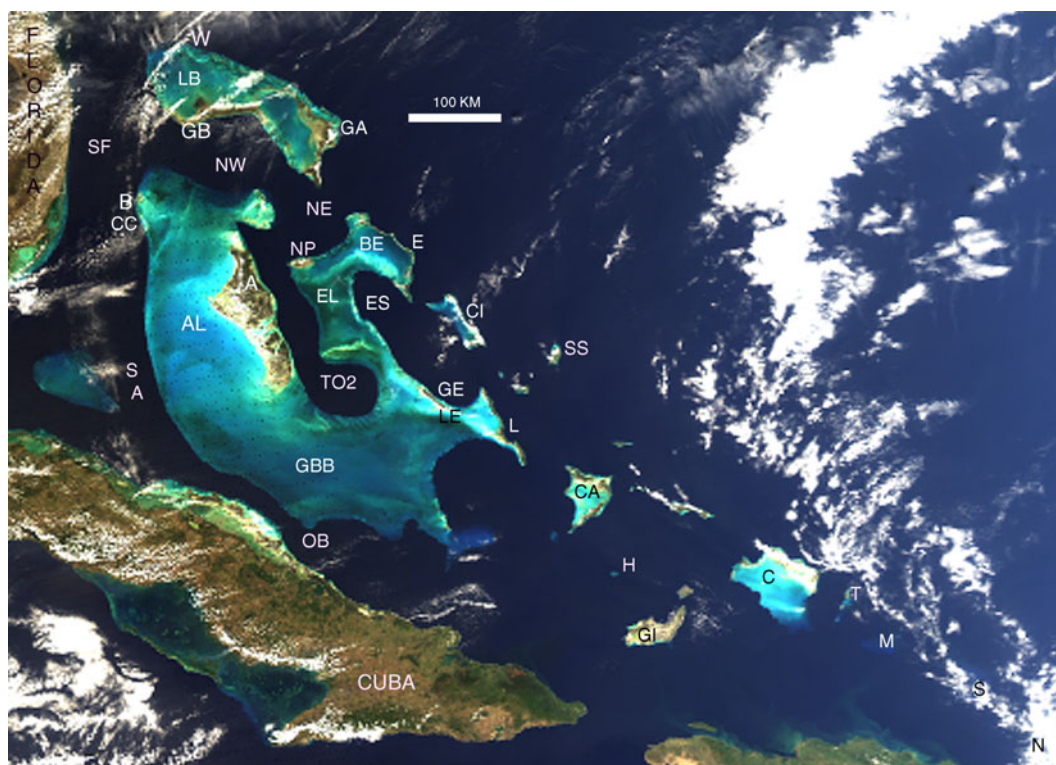
### Definition

“Bahamas” denotes the Bahamas Archipelago of 700 islands and approximately 2,400 cays and rocks that stretches from 27°36′ to 19°52′N latitude and from 79°05′ to 68°42′W longitude, a distance of about 1,300 km (Figure 1). That includes the Caicos and Turks Islands as well as Mouchoir, Silver, and Navidad Banks that are geographically, geologically, and ecologically part of the Bahamas, although separate entities politically. The land area of the Bahamas Commonwealth is 13,900 km<sup>2</sup>, home to some 306,000 people on 30 of the islands and host to 4.6 million tourists annually (Government of the Bahamas). By far the largest part of the Bahamas, some 155,000 km<sup>2</sup>, lies beneath the sea (Newell, 1955). Of interest here are the vast shallow (<20 m) banks, the Great Bahama Bank (GBB), the Little Bahama Bank (LBB), and the smaller banks extending far to the southeast, encompassing about

125,000 km<sup>2</sup> (Bergman et al., 2010). The shallow banks from Caicos to Navidad Bank add another 10,200 km<sup>2</sup>. These banks are the largest area of coral-reef development in the Western Hemisphere. The reefs were an important resource for the indigenous Lucayans and were noted early by European explorers, beginning with C. Columbus.

### Introduction

The Bahama Banks, surrounded by deep water on all sides, provide excellent analogs for the numerous isolated carbonate platforms in the geological record. Sedimentologic studies in the Bahamas have been extensive, for example, by Black (1933), Smith (1940), Illing (1954), Cloud (1962), Purdy (1963), Ball (1967), Shinn et al. (1969), Hardie (1977), Harris (1979), Hine et al. (1981), Droxler and Schlager (1985), and numerous others. Basically, the broad platform interiors are blanketed by pellet and grapestone (aggregate grains, typically of pellets) sand with increasing mud content in the lee of larger islands on the windward margins (Traverse and Ginsburg, 1966; Enos, 1974). The windward sides of the islands are the favored sites of reefs and skeletal sands. Where island



**Bahamas, Figure 1** Satellite image of the Bahamas and adjacent banks. A Andros Island; AL Andros lobe of GBB; B Bimini islands; BE Bight of Eleuthera; C Caicos platform; CA Crooked-Acklins platform; CC Cat Cays; CI Cat Island; E Eleuthera Island; EL Exuma lobe of GBB; ES Exuma Sound; GA Great Abaco Island; GB Grand Bahama Island; GBB Great Bahama Bank; GE Great Exuma Island; GI Great Inagua Island; H Hogsty Reef; L Long Island; LB Little Bahama Bank; LE Little Exuma; M Mouchoir Bank; N Navidad Bank; NE Northeast Providence Channel; NP New Providence Island (Nassau); NW Northwest Providence Channel; OB Old Bahamas Channel; S Silver Bank; SA Santaren Channel; SF Straits of Florida; SS San Salvador Island; T Turks platform; TO<sup>2</sup> Tongue of the Ocean; W Walker's Cay. Image courtesy of NASA/GSFC, MODIS Rapid Response.

and bank configuration focus tidal currents, ooid shoals are formed.

Tectonic and stratigraphic studies have established that up to 10 km of largely shallow-water carbonates, Jurassic to Holocene in age, overlie rifted Jurassic transitional crust in the NW Bahamas and oceanic crust SE of Tongue of the Ocean (TOTO, Sheridan et al., 1988), although others have argued for African continental crust (Mullins and Lynts, 1977). A carbonate “megabank” developed in the Early Cretaceous that may have included the Bahamas, Florida, and Yucatan (Austin and Schlager, 1988). This bank was fragmented into smaller platforms separated by subsiding blocks in the mid-Cretaceous. The southern part was further fragmented during collision with Cuba in Late Cretaceous–Middle Eocene (Masafello and Eberli, 1999). Seismic stratigraphy shows that leeward lateral accretion of sediment derived from the bank tops has filled such depressions, merging platform fragments during the Cenozoic to form the GBB (Eberli and Ginsburg, 1987, 1989; Masafello and Eberli, 1999). Deep channels (Straits of Florida, Santaren Channel, Old Bahamas Channel, Providence Channels) and reentrants (TOTO, Exuma Sound) remain. These dissect the banks and isolate them from terrigenous input except for wind-blown dust that reddens the soils.

Coral reefs were common around the margins of the Bahama Banks at least as far back as the Pliocene (Beach and Ginsburg, 1980). Pleistocene reefs are exposed on most of the major islands (Cant, 1977), some extending to 5 m above present sea level (Hearty, 1998). Lithified Pleistocene eolianite dune ridges form the bulk of the Bahaman islands, however, reaching 63-m elevation on Cat Island (Government of the Bahamas). Subtidal Pleistocene deposits extend up to 6 m above sea level on the large islands. Multiple Holocene beach-accretion ridges, anchored by Pleistocene buttresses, form many low-lying areas. Origins from dunes, beaches, and reefs dictate that the largest islands (Andros, Eleuthera, Great Abaco) and highest (Cat Island) lie at the eastern margins of the banks, where tides, trade winds, and wave fetch maximize skeletal sediment production (Ball, 1967).

Most islands have multiple nested rows of Pleistocene dunes, generally younging toward the windward margin. This is well illustrated on New Providence and adjacent islands where six prominent ridges are visible on topographic maps (Hearty and Kindler, 1997). Strings of small cays formed by eroded dunes near the shelf break are common around the Bahamas, even on the shallower leeward margins, e.g., from Bimini south beyond Cat Cays. Similarly, the eroded remnants of dunes, beaches, and reefs dominate the submarine topography at the margins of the Bahama Banks. This combination of linear, arcuate, and spur-and-grove ridges are the substrate for modern reef growth, as well as vast areas of coral-encrusted hard grounds.

Environmental parameters that impact the reefs most directly include climate and hydrology. Bahaman climate ranges from humid subtropical with dry winters in the

NW (18–28°C monthly average temperature, 73–79% humidity, 135.5 cm annual rainfall on Grand Bahama Island) to subarid tropical in the SE (25–34°C, 18–25%, 60.4 cm/year, Caicos). About half of the area lies within the tropics; the Tropic of Cancer bisects Little Exuma Island. Sea-surface temperatures range from 21.7 to 28.3°C annually on the Andros lobe of GBB (Cloud, 1962) compared to 26–29°C on Caicos Bank.

The Bahamas lie in the northeasterly trade winds belt, but continental low pressures over North America produce predominately southeasterly winds during the warmer months (Smith, 1940). Continental cold fronts occasionally impinge on the northwestern Bahamas in winter, producing strong NW winds and cooling the bank water with air temperatures down to 3°C. Hurricanes struck the Bahamas–Turks area 121 times from 1901 to 1963 (compiled from Cry, 1965), an average of two per year. Twenty-one of these storms passed directly over Andros Island. The damage to reefs from wave pressure and sediment abrasion can be severe, although it is quite variable, depending on storm intensity, direction, duration, and frequency.

The Bahamas are bathed by the north equatorial current that bifurcates to produce currents of 30–42 cm/s along the eastern islands and 46 cm/s in Old Bahama Channel to the south (Carew and Mylroie, 1997). The Gulf Stream skirts the western Bahamas with velocities up to 200 cm/s (Bergman et al., 2010). The range of semidiurnal tides is about 1 m at the platform margins everywhere in Bahamas. Resonance in the deep embayments, such as TOTO, can amplify the tides and produce strong currents at the margins, generating ooid shoals instead of reefs (Ball, 1967). Water at the bank margins has normal marine salinities, about 36 ppt, but sluggish circulation on the larger banks, where residence time can reach 240 days, produces salinities reaching 43 ppt in the hotter months (Broecker and Takahashi, 1966).

### Reef distribution

Bank/barrier reefs in the Bahamas occur almost exclusively on the windward (eastern) sides of banks. They are best developed on margins facing the open Atlantic swell (Rankey et al., 2009) and where large islands provide protection from the flux of bank-top water. The fluctuations of bank water in temperature, salinity, nutrients, and turbidity are detrimental to most corals, although patch reefs thrive on some areas of the banks. Lee margins, where wave energy is minimal and wind-driven flux of bank water is maximum, have few reefs that are small and deeper.

Reefs occur intermittently for 160 km along the north-east-facing margins of LBB, from beyond Walker’s Cay at the north to Elbow Cay at the middle of Great Abaco Island. The narrow, steeply sloping shelf further south, which faces ESE, has few reefs (Feingold et al., 2003; Rankey et al., 2009). Reefs on the LBB extend 220 km further north than Florida reefs despite the partiality of the Gulf Stream to Florida. Coral cover averaged only 14%



in the Abaco reefs, which contain 36 scleractinian species (Feingold et al., 2003).

The Andros reef tract bordering TOTO on GBB is 217 km long, a close second to the more continuous Belize reef tract, longest in the Atlantic. Coral cover in 1997–1998 was  $38 \pm 17\%$  for reef crests ( $<3.5$  m), the highest in the Atlantic, and  $25 \pm 14\%$  for fore-reef transects (5.5–12.5 m; Kramer, 2003). Disease and extensive bleaching events (stress-induced loss of symbiotic zooxanthellae) in 1998 and 2005 reduced cover to  $<10\%$  on some fore reefs (Kramer, 2008). Reefs in the Berry Islands are limited to small fringing reefs and near-shore patch reefs, despite the very exposed setting (Figure 1).

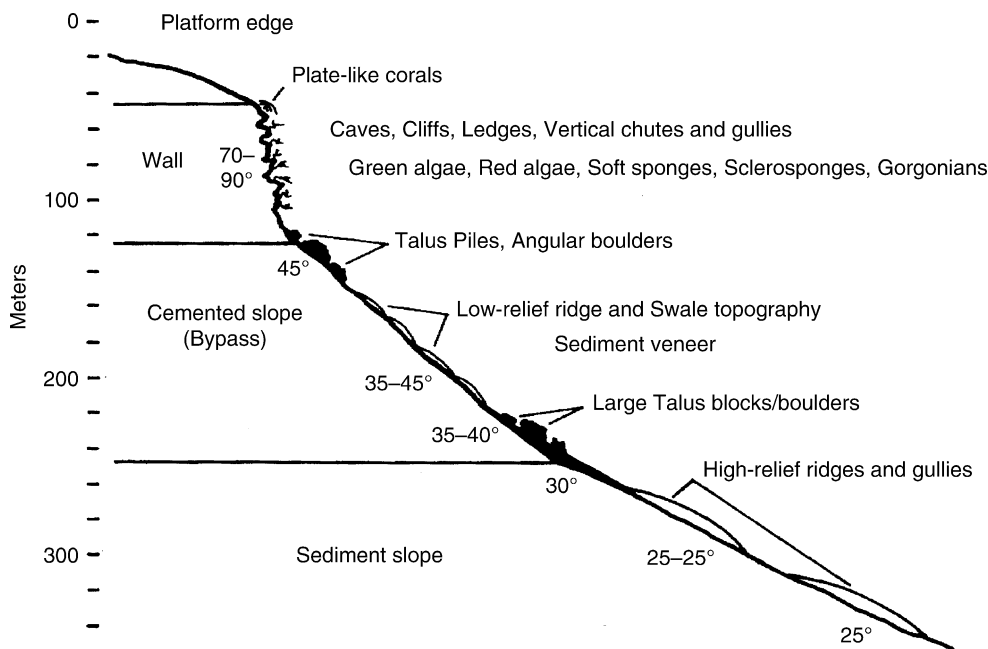
The Exuma Islands' setting is similar to Andros, facing deep water of Exuma Sound. However, bank/barrier reefs are virtually absent, apparently because of the small size of the islands and the many tidal channels into the bank interior. Corals, gorgonians, and sponges colonize hard substrates in tidal channels and on the narrow shelf windward of the islands (Chiappone et al., 1997a). Patch reefs are abundant in the platform interior (unpublished data; Taft et al., 1968).

At the NE corner of GBB, Eleuthera Island, 135 km long, faces the abyssal open Atlantic Ocean. Flourishing shallow reefs that fulfilled expectations of this setting in 1990 were reduced to algal-dominated shadows by 2000 and have not recovered (Craig Dahlgren, pers. commun.). Reef development was continuous along the east-facing southern half of the island; gaps appeared further north. Pigmented skeletal fragments of the abundant encrusting foraminifer *Homotrema rubrum* produce the famous pink beaches of Eleuthera.

Cat Island, 85 km long and facing NE into the open Atlantic, has well-developed reefs, except where oceanic waves impinge directly on the sea cliffs. Long Island, comparable in size and setting at the eastern extremity of GBB, has well-developed bank/barrier reefs and patch reefs on the narrow shelf along the north three-quarters of the windward margin. Imagery is poor further south, but lack of breakers suggests lack of barrier reefs.

Of the numerous isolated banks, only two have been studied in any detail, the small San Salvador bank ( $\sim 150$  km<sup>2</sup>; Peckol et al., 2003) and the largest, Caicos platform (7,800 km<sup>2</sup>; Wanless and Dravis, 1989; Sullivan et al., 1994; Chiappone et al., 1996; Rankey et al., 2009). These studies as well as anecdotal accounts and imagery analysis (Google Earth with widely variable resolution) show that all of the banks have bank/barrier reefs and patch reefs where substantial shelf exists. Reefs are best developed on NE-facing margins, which are perpendicular to the predominant wave direction in the adjacent North Atlantic. However, shallow reefs are present on all but the westernmost, leeward margins. Even here are a few smaller, deeper reefs that have not aggraded to sea level (Rankey et al., 2009).

Patch reefs are rare on much of the Andros lobe of GBB and in the Bight of Eleuthera, probably because of the soft, muddy substrates and elevated salinities. In contrast, on the less restricted Exuma lobe and southeastern GBB, where hard substrates are plentiful, patch reefs abound, ranging in size from a few coral heads to reef clusters 1,200 m in length with areas over 1 km<sup>2</sup>. Density of patch reefs visible on satellite imagery ( $>$ about 10 m diameter) on the Exuma lobe is 25 per km<sup>2</sup> (unpublished data).



**Bahamas, Figure 2** Schematic profile of Bahaman platform-margin slopes. No vertical exaggeration! From Grammer and Ginsburg (1992).

Flourishing reefs attain relief of 4 m or more. At the margins of platforms, large and small patch reefs are common on the narrow shelves between bank/barrier reefs and islands.

The Bahamas even boast one atoll, Hogsty Reef, north of Great Inagua (Milliman, 1967).



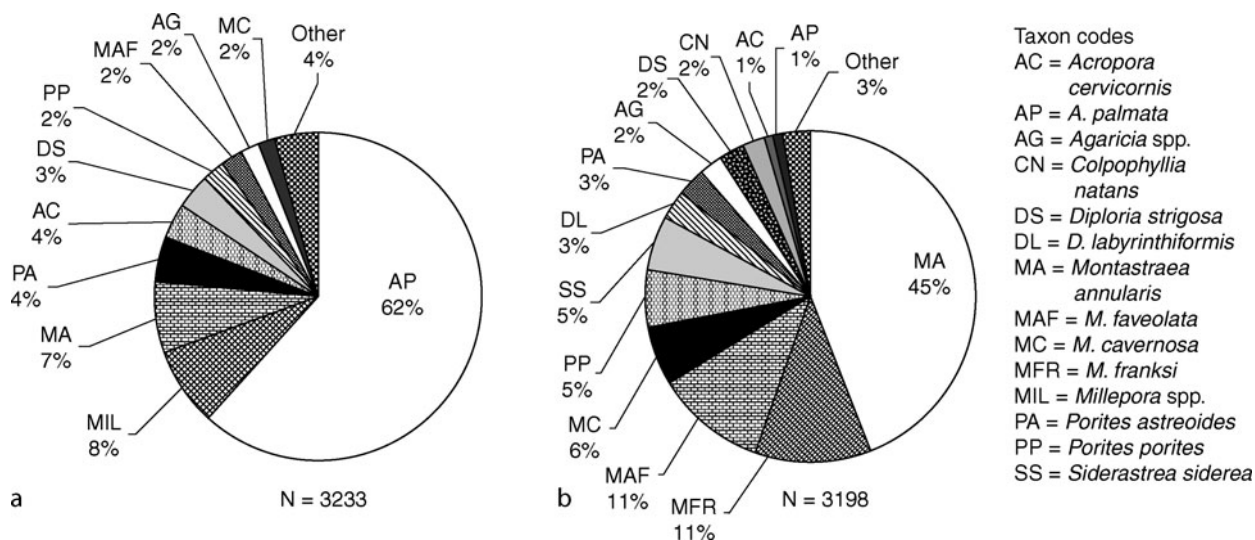
**Bahamas, Figure 3** *Acropora palmata*, aka moosehorn or elkhorn coral, the reef-crest dominant. Exumas National Park, Cambridge Cay. Courtesy of Tim Taylor.

Stromatolites, layered mounds of varied shapes up to 2.5 m high composed of carbonate sand bound by microbial mats and lithified by marine carbonate cement, form transverse “reefs” or sediment dams in high-energy tidal channels (Dill et al., 1986). Similar structures also occur in a sandy embayment and intertidal beaches (Reid et al., 1995), but all 14 localities studied are in the Exuma Islands.

Deeper waters in the Bahamas host major coral growths, commonly called reefs, although few have significant constructional relief. A typical margin of a Bahaman platform has a shallow slope break at a barrier reef or the edge of the flat-topped bank. A narrow slope descends in a series of erosional and constructional terraces to a sharp slope break at –25 to –60 m, where a near-vertical “wall” plunges for about a 100 m (Figure 2; Grammer and Ginsburg, 1992). The wall is probably a Pleistocene sea cliff, buried at the base by cemented rubble from above. This configuration is obscured on many leeward margins by thick drifts of sediment washed off the bank tops. Rocky terraces at the top of the wall support thickets that include 69 types of sponges, 28 species of corals, 27 species of octocorals, and *Millepora alcicornis* (Bunt et al., 1981). The vertical wall, within the “mesophotic zone,” is covered by a profusion of sponges (Maldonado and Young, 1996) as well as corals and octocorals, which have not been studied. Sponges, which extend beyond depths of 500 m, include the light-shunning sclerosponges that secrete massive carbonate skeletons (Hartman, 1980).

#### Reef biota and zonation

The dominant frame builder of most shallow bank/barrier reefs of the Bahamas, as throughout the Caribbean, has been *Acropora palmata* (Figure 3). Despite marked decline over several decades, it constituted 62% of the corals ( $\geq 25$  cm) counted from reef crests of the Andros



**Bahamas, Figure 4** Relative abundance of stony corals ( $\geq 25$  cm diameter) in the Andros reef tract. (a) Reef crests (<3 m deep). (b) Fore reefs (8–12 m deep). From Kramer et al. (2003).

**Bahamas, Table 1** Corals species of the Bahamas<sup>a</sup>

| Class/order                          | Family                          | Genus and species                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                     |
|--------------------------------------|---------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Class Hydrozoa/Subclass Hydroidolina |                                 |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Order Anthoathecatae                 |                                 |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Suborder Filifera                    | Stylasteridae                   | <i>Stylaster roseus</i> (Pallas, 1766)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                |
| Suborder Capitata                    | Milleporidae                    | <i>Millepora alcicornis</i> Linnaeus, 1758<br><i>M. complanata</i> Lamarck, 1816                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
| Class Anthozoa/Subclass Hexacorallia |                                 |                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                       |
| Order Scleractinia                   | Astrocoeniidae                  | <i>Stephanocoenia intersepta</i> (Lamarck, 1816)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
|                                      | Pocilloporidae                  | <i>Madracis decactis</i> (Lyman, 1859)<br><i>M. formosa</i> Wells, 1973<br><i>M. auretenra</i> Locke, Weil and Coates, 2007                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                           |
|                                      | Acroporidae                     | <i>Acropora cervicornis</i> (Lamarck, 1816)<br><i>A. palmata</i> (Lamarck, 1816)<br><i>A. prolifera</i> (Lamarck, 1816)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |
| Suborder Fungiina                    | Agariciidae                     | <i>Agaricia agaricites agaricites</i> (Linnaeus, 1758)<br><i>A. agaricites carinata</i> Wells, 1973<br><i>A. agaricites danai</i> ME & H, 1860<br><i>A. agaricites purpurea</i> (Lesueur, 1821)<br><i>A. fragilis fragilis</i> Dana, 1846<br><i>A. grahamae</i> Wells, 1973<br><i>A. humilis</i> Verrill, 1902<br><i>A. lamarcki</i> ME & H<br><i>A. tenuifolia</i> Dana, 1846<br><i>A. undata</i> (Ellis and Solander, 1786)<br><i>Leptoseris cucullata</i> (Ellis and Solander, 1786)                                                                                                                                                                                               |
|                                      | Siderastreidae                  | <i>Siderastrea radians</i> (Pallas, 1766)<br><i>S. siderea</i> (Ellis and Solander, 1786)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |
|                                      | Poritidae                       | <i>Porites astreoides</i> Lamarck, 1816<br><i>P. branneri</i> Rathbun, 1888<br><i>P. porites furcata</i> Lamarck, 1816<br><i>P. porites porites</i> (Pallas, 1766)<br><i>Colpophyllia natans</i> (Houttuyn, 1772)<br><i>Diploria clivosa</i> (Ellis and Solander, 1786)<br><i>D. labyrinthiformis</i> (Linnaeus, 1758)<br><i>D. strigosa</i> (Dana, 1846)<br><i>Favia fragum</i> (Esper, 1795)<br><i>Manicina areolata areolata</i> (Linnaeus, 1758)<br><i>M. areolata mayori</i> Wells, 1936<br><i>Montastraea annularis</i> (Ellis and Solander, 1786)<br><i>M. faveolata</i> (Ellis and Solander, 1786)<br><i>M. franksi</i> (Gregory, 1895)<br><i>M. cavernosa</i> Linnaeus, 1767 |
| Suborder Faviina                     | Faviidae                        | <i>Dendrogyra cylindrus</i> (Ehrenberg, 1834)<br><i>Dichocoenia stellaris</i> ME & H, 1848<br><i>D. stokesi</i> ME & H, 1848<br><i>Meandrina meandrites meandrites</i> (Linnaeus, 1758)<br><i>Isophyllastrea rigida</i> (Dana, 1846)<br><i>Isophyllia sinuosa</i> (Ellis and Solander, 1786)<br><i>Mussa angulosa</i> (Pallas, 1766)<br><i>Mycetophyllia aliciae</i> Wells, 1973<br><i>M. danaana</i> ME & H, 1849<br><i>M. ferox</i> Wells, 1973<br><i>M. lamarckiana</i> ME & H, 1848<br><i>M. reesi</i> Wells, 1973<br><i>Scolymia cubensis</i> ME & H, 1849<br><i>S. lacera</i> (Pallas, 1766)                                                                                    |
|                                      | Meandrinidae                    | <i>Astrangia solitaria</i> (Lesueur, 1817)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                            |
| Suborder Caryophylliina              | Rhizangiidea<br>Caryophylliidae | <i>Eusmilia fastigiata</i> (Pallas, 1766)                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                             |

Note: ME &amp; H refers to Milne-Edwards and Haime

<sup>a</sup>After Chiappone et al. (1996, 1997a), Bunt et al. (1981); updates from J. C. Lang (pers. comm.)

Taxonomic names are consistent with Integrated Taxonomic Information System.



reef tract in 1998 (Kramer et al., 2003), although it is much reduced today. It was less dominant elsewhere: 35% in Turks and Caicos reefs (Riegl et al., 2003) and 13–18% at San Salvador (Peckol et al., 2003). Abaco reefs on LBB are low-relief structures dominated by *Porites astreoides*, *Diploria* spp., and *Millepora* spp. These northernmost reefs in the Atlantic, except for the Bermuda outlier, are apparently beyond the optimal range of acroporids. Arborescent *A. cervicornis* (staghorn coral) once formed vast thickets in many reefs, but they are largely a memory, victims of disease and destruction.

In shallow fore-reef and back-reef environments, massive heads of the *Montastraea annularis* species complex (MASC) are dominant. The complex encompasses three similar sympatric forms, considered valid species by Weil and Knowlton (1994), but overlapping morphologically in the Bahamas (Fukami et al., 2004). Prior studies treated *M. franksi* and *M. faveolata* as environmentally controlled variants of *M. annularis* (boulder coral) and some current work continues this practice. In the Andros fore reefs, 67% of the counts of corals  $\geq 25$  cm were MASC in 1988; 45% were *M. annularis* S.S. (Figure 4; Kramer et al., 2003). Given the robustness of MASC colonies, the spatial dominance would be even greater. *Montastraea* is less

dominant in other surveyed Bahaman reefs, including Abaco, although this is well within its geographic range.

Common accessory corals on all reefs include *Porites astreoides*, *P. porites*, *Agaricia* spp., and *Diploria* spp., and any of these may dominate on a specific reef. *Siderastrea siderea* is also nearly ubiquitous, but is more common in deeper and more sheltered settings. The hydrozoans, *Millepora alcicornis* and *M. complanata*, occur throughout the reefs with abundances as high as 20% (Abaco, Feingold et al., 2003). A complete list of observed Bahaman corals includes approximately 43 species (Table 1), comparable to the most diverse (and well studied) sites in the western Atlantic (Chiappone et al., 1996; Kramer, 2003).

Among patch reefs, MASC is dominant with varying abundances of *Diploria* spp., *Porites porites*, *P. astreoides*, and *Siderastrea siderea*. *Millepora alcicornis* is always

#### Bahamas, Table 2 Octocorals of the Bahamas<sup>a</sup>

##### Order Alcyonacea

##### Family Briareidae

*Briareum asbestinum* (Pallas, 1766)

##### Family Anthothelidae

*Erythropodium caribaeorum* (Duchassaing & Michelotti, 1860)

##### Family Plexauridae

*Eunicea calyculata* (Ellis & Solander, 1786)

*E. clavigera* Bayer, 1961

*E. fusca* Duchassaing & Michelotti, 1860

*E. knighti* Bayer, 1961

*E. laciniata* Duchassaing & Michelotti, 1860

*E. laxispica* (Lamarck, 1815)

*E. mammosa* Lamouroux, 1816

*E. palmeri* Bayer, 1961

*E. succinea* (Pallas, 1766)

*E. tourneforti* Milne-Edwards & Haime, 1857

*Muricea atlantica* (Riess in Kükenthal, 1919)

*M. elongata* Lamouroux, 1821

*M. laxa* Verrill, 1864

*M. muricata* (Pallas, 1766)

*Muriceopsis flavida* (Lamarck, 1815)

*Plexaura flexuosa* Lamouroux, 1821

*P. homomalla* (Esper, 1792)

*Plexaurella dichotoma* (Esper, 1791)

*P. grisea* Kunze, 1916

*P. fusifera* Kunze, 1916

*P. nutans* (Duchassaing & Michelotti, 1860)

*Pseudoplexaura flagellosa* (Houttuyn, 1772)

*P. porosa* (Houttuyn, 1772)

##### Family Gorgoniidae

*Gorgonia flabellum* Linnaeus, 1758

*G. ventalina* Linnaeus, 1758

*Pseudopterogorgia acerosa* (Pallas, 1766)

*P. americana* (Gmelin, 1971)

*P. bipinnata* (Verrill, 1864)

*P. elisabethae* Bayer, 1961

*P. kallos* (Bielschowsky, 1918)

*P. rigida* (Bielschowsky, 1929)

*Pterogorgia anceps* (Pallas, 1766)

*P. citrina* (Esper, 1792)

*P. guadalupensis* Duchassaing & Michelotti, 1846



**Bahamas, Figure 5** Abundant octocorals and sponges, top of The Wall, Wax Cay, Exumas. Depth 25 m. Courtesy of Tim Taylor.

<sup>a</sup>After Chiappone et al. (1997b) and Bunt et al. (1981).

present, especially as encrusters on senescent patches. Patch-reef coral diversity is high, e.g., 26 species in the Exumas (Chiappone et al., 1997a), despite the absence of acroporids. Pante et al. (2008) reported a decline in coral cover from 13 to 3%, accompanied by extensive rubble production, on an Exuma patch reef between 1991 and 2004. MASC was the biggest loser, although it remained dominant, whereas *M. alcicornis* gained both in coverage and number of colonies.

Corals on the deeper terraces and the wall are also dominated by MASC (45% of coral cover) and *Siderastrea siderea* (20%) (Bunt et al., 1981). The 26 species reported include all of the forms abundant on the shallow reefs (Table 1), except the acrophobic acroporids.

Atlantic reefs contain many more octocorals and sponges (Figure 5) than Pacific reefs, which have much higher coral diversity. Thirty-five species of octocorals have been identified from the Bahamas (Table 2; Bunt et al., 1981; Chiappone et al., 1997b). Wiedenmayer (1980) recorded 84 species or forms of sponges from shallow rock and reef substrates. Curiously, the brightly colored, ubiquitous, and prodigious reef/rock borer, *Cliona*, was not among them. Of the 19 deep-water sponge genera mentioned anecdotally by Maldonado and Young (1996), 16 are not recorded from shallow water.

Crustose coralline algae, including *Lithophyllum congestum* and *Porolithon pachydermum*, are common in Bahaman reefs (Adey, 1978), constituting 30% of the total algal cover (Kramer, 2003). They construct cups and linear “algal ridges” on Great Inagua and the Plana Cays (east of Crooked–Acklins platform), although ridges are lacking further north (Adey, 1978). Arborescent *Jania*, *Amphiroa*, and *Neogoniolithon* contribute generously to

the sediment accumulation, if not to the mass of the reefs. Calcified green algae, notably *Halimeda opuntia*, are the major contributors to the skeletal sand around reefs because of their high production and disarticulation rates. Multitudes of fleshy macroalgae populate the reefs. They are considered a sign of declining reefs, as they can outcompete stony corals for space and light, especially since the catastrophic die-off of the algal-grazing urchin, *Diadema antillarum*, in 1983 (Kramer, 2003). Andros reef tract had the highest “macroalgal index” (relative abundance x colony height) reported from the Atlantic to 1999 (Kramer, 2003), although later surveys in the central and western Caribbean reported indices up to 40% higher (AGRRA database, <http://www.agrra.org>).

Reefs are the shelter, grazing range, home, or hunting grounds of many organisms. Prominent in the Bahamian reefs are multitudes of fish (Kramer, 2003), urchins, lobsters, shrimp, worms, bivalves, gastropods, bryozoans, anemones, and foraminifers. Particularly important in degrading the reefs into sediment are various bioeroders that include fungi, cyanobacteria, sponges, lithophagid and pholad bivalves, chitons, boring and rasping gastropods, sipunculid and polychaete worms, barnacles, boring and rasping echinoids, parrot fish, and many other grazing fish.

### Reef health

Worldwide decline of reefs, one of the most diverse of ecosystems, is causing grave concern and intensive research. A reef-health index based on 13 parameters including coral cover, mortality, and disease; macroalgal index; and fish populations was devised from the initial AGRRA survey of Atlantic reefs (Kramer, 2003). Andros had the worst health index of 17 Caribbean and Gulf sites



**Bahamas, Figure 6** *Porites*-dominated reef; the future of Bahaman reefs? Cochinis Bank, southeastern GBB (Courtesy of Tim Taylor).



compared and Abaco the third worst. Turks/Caicos ranked “average.” Coral bleaching, such as the worldwide event during El Niño conditions in 1998, and consequent diseases may be the most destructive agents. Since the survey, a new threat to the fish population, and perhaps the entire reef ecosystem, has arisen through the accidental introduction of the voraciously carnivorous lionfish, *Pterois volitans*, from the Indo-Pacific. Despite this gloomy picture, it seems possible that Bahaman reefs, now near the low-temperature limit, may benefit from global warming by shifting toward a more tropical ecology.

AGRRA surveys in the Bahamas, as elsewhere, show that recruitment rates of “brooder” corals such as *Porites* spp. and *Agaricia* spp. are much higher than those of broadcast spawners, including *Acropora* spp. and *Montastrea* spp., the former dominants on shallow and deep reefs, respectively (Kramer, 2003). If this portends a shift in reef populations, perhaps the words of Opdyke et al. (2007), “I have seen the future, and it is *Porites*,” are prophetic. Nevertheless, Bahaman reefs could remain productive and beautiful (Figure 6).

## Summary

The Bahama Banks and adjacent platforms, the largest area of coral-reef development in the Western Hemisphere, are excellent analogs for the isolated carbonate platforms in the rock record. Bank/barrier reefs line the windward margins of most platforms. Patch reefs are widely distributed across those platforms with more open circulation and hard substrates. Into this century *Montastrea annularis* “complex” dominated the fore reef and patch reefs; *Acropora palmata* the bank/barrier-reef crest. Octocorals, sponges, and calcareous algae are important and diverse components of Bahaman reefs.

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## Cross-references

Acropora  
 Algae, Coralline  
 Banks Island: Frasnian (Late Devonian) Reefs In Northwestern Arctic Canada  
 Eolianite  
 Florida Keys  
 Foraminifera  
 Halimeda  
 Ooids  
 Patch Reefs: Lidar Morphometric Analysis  
 Residence Time  
 Sponges  
 Stromatolites  
 Western Atlantic/Caribbean, Coral Reefs

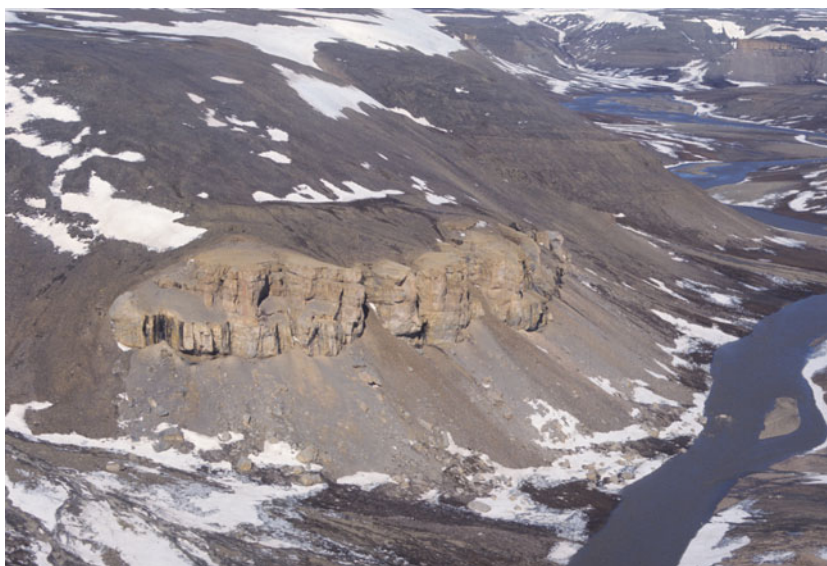
## **BANKS ISLAND: FRASNIAN (LATE DEVONIAN) REEFS IN NORTHWESTERN ARCTIC CANADA**

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During the Frasnian (385.3–374.5 my), stromatoporoid sponge and coral reefs were restricted to about 5,000 km<sup>2</sup> of Banks Island (Thorsteinsson and Tozer, 1962). The

more than 2,000 km long preceding Middle Devonian barrier reef platform, extending westward from Greenland, lay buried in thick sands, silts, and muds. Banks Island reefs are remarkable for several reasons: (a) they were built up on the margins of an equatorial super delta, fringed by one of the oldest coastal lowland forests, whose margins harbored primitive-jawed placoderm fishes, and some of the first amphibians; (b) they flourished in the early and mid-Frasnian, prior to the Frasnian–Famennian global mass extinction events; (c) the reefs grew in four cycles,



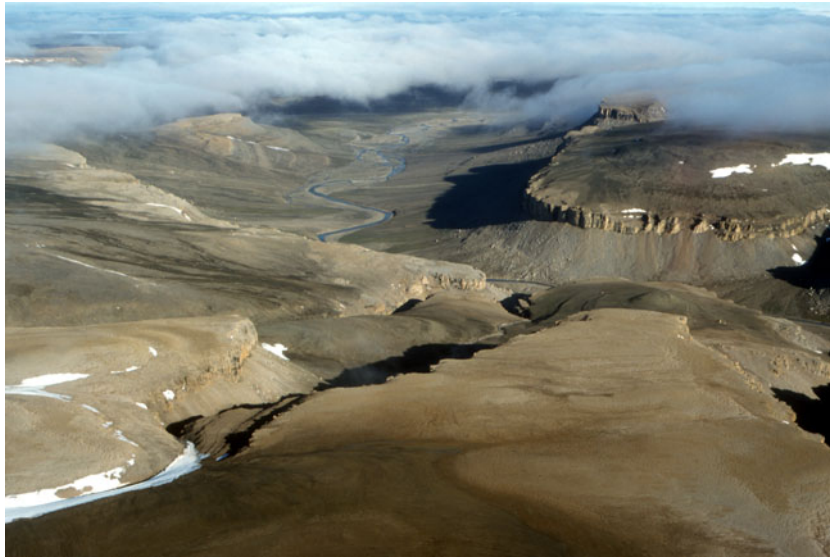
**Banks Island: Frasnian (Late Devonian) Reefs In Northwestern Arctic Canada, Figure 1** Large patch reef, ca. 400 m diameter, B-level, Mercy Formation, located along the north banks of the lower Mercy River tract (NTS 88F/3, 578:176) facing reef B62.



**Banks Island: Frasnian (Late Devonian) Reefs In Northwestern Arctic Canada, Figure 2** The north end of Gyr Falcon Bluff close to the southern edge of Mercy Bay, Banks Island: the ca 60 m high bluff consists of two large C-level reefs that almost fused, a northern reef (visible) and a southern reef, hidden in the southern background in this helicopter view.

reflecting global eustatic sea level changes, probably related to glaciations in Brazil; and (d) the reefs reflected back-stepping events to the east during sea level highstands, and westward retreat at lowstands. The Frasnian is generally characterized by a lower diversity reef ecosystem than seen in the preceding Middle Devonian, with the Devonian reef ecosystem collapsing step-wise toward the end of the Frasnian Mass Extinctions (Copper, 2002) (Figures 1 and 2).

The Banks reef builders were dominated by exquisitely preserved stromatoporoid sponges as massive, platy forms meters thick, and in large domal forms that inhabited the open ocean, high energy fore-reef zone. In the back-reef lagoons, or off-reef deeper waters, stromatoporoids and corals grew as branching structures (Copper and Edinger, 2009). The corals and sponges probably had photosymbionts, as do many modern reef dwellers. The digitate stachyodid and slender matchstick-sized amphiporid



**Banks Island: Frasnian (Late Devonian) Reefs In Northwestern Arctic Canada, Figure 3** The carbonate platform levels B, C and D of the Frasnian Mercy Formation as seen from the air looking northwest along the East Mercy River branch. The B level reef is in the upper left background, and C-D levels in the foreground.



**Banks Island: Frasnian (Late Devonian) Reefs In Northwestern Arctic Canada, Figure 4** D-level upper 11A and 11B reefs in the Mercy Fm along the M'Clure River, northeast coast Banks Island: these reefs rest on top of siliciclastics and are buried by deltaic siliciclastics (NTS 88C/14, N74° 0.371', W117° 0.727').



stromatoporoids grew in upright bushes, usually on fine lime mud substrates that indicate sheltered environments.

The Banks reef tabulate and rugose corals were more diverse than the stromatoporoids, but volumetrically <30% of the reef mass, though some patch reefs were monospecific thamnoporid corals. The calcitic microstructure of Banks corals is commonly better preserved than modern day scleractinian corals. Solitary cup corals were very rare on Banks Island. In overall construction strategy, rugose corals were dendroid, phaceloid, cerioid, thamnasterioid, and aphroid forms, but lacked the meandroid ‘brain coral’ morphology of modern taxa. For the tabulate corals, dominant were the alveolitids (flat- to dish-shaped to cup-shaped, like the living lettuce coral *Agaricia*), coenitids (flat or branching), and thamnoporids (branching, almost identical to living *Porites porites*). The corals were more abundant as thickets, usually reef-flanking or biostromal, or as a lesser component within the fore-reef or reef flat. Unique for the Devonian, some corals and stromatoporoids grew on foundered tree trunks, the oldest known in the fossil record. Except for rare armored fragments and teeth, fishes were scarce in the Banks reef setting, as were shelly brachiopods, calcareous green and red algae.

Patch reefs ranged from a few meters in height and diameter to massive rounded to elongate mounds to a kilometer or more long and 30–50 m in composite height (Thorsteinsson and Tozer, 1962; Copper and Edinger, 2009) (Figure 4), found throughout the 220 m thick carbonate succession of the Mercy Bay Formation. Platform reefs, with a reef flat and slope up to ca. 30°, developed only at one Frasnian sea level highstand, and these were irregular in plan view, with scalloped edges possibly fringing delta lobes (Figure 3). Reefs generally initiated growth on coral debris.

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## BANKS, JOSEPH (1743–1820)

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Banks, a founding father of natural science and co-founder of Australia, was born in London, Great Britain, on February 13, 1743, the only son of a wealthy landowner. He married Dorothea Hugesson on March 23, 1779. He

died in Isleworth, London, on June 19, 1820, aged 77. Banks devoted his entire adult life toward the advancement of science.

On his triumphant return from Captain Cook’s first great voyage in 1771, the young Banks was famously dubbed “The Botanic Macaroni” and “The great South Sea caterpillar.” Over the next 50 years, however, this satiric “caterpillar” was transformed into the “Bath Butterfly” by his royal investiture as Knight Commander of the Order of the Bath in 1795 (Figure 1). He was honored for his remarkable achievements in an era of enlightened human endeavor with his: knighthood (1781); membership of the Privy Council (1797); and his unmatched 4-decade term as President of the Royal Society (1778–1820). Banks galvanized the great scientific minds of his time, systematized natural history collection, and promoted foundation projects.

His early credentials were botanical collections (in the British Museum) from expeditions to: Labrador and Newfoundland (1766–1767); the southern ocean with Captain Cook (1768–1771); and Iceland and the New Hebrides (1772). Subsequently, he funded and encouraged others to gather and catalogue specimens of plants and animals throughout the world. Using his unofficial directorship of Kew Gardens in London to explore the economic and social benefits of plants, he created one of the world’s great public gardens.

Banks was a natural leader, a rare individual with no political leanings or ambitions. Though a favorite of



**Banks, Joseph (1743–1820), Figure 1** Sir Joseph Banks in full regalia as President of the Royal Society, by Thomas Phillips, 1808–1809.

King George III, he maintained a friendly correspondence with Benjamin Franklin in revolutionary America. He did not discriminate between British and foreign scientists. He helped maintain scientific relations with France during the French Revolution and the Napoleonic Wars. Banks was greatly respected by Carl Linnaeus, who devised the binomial naming system used today for all plants and animals. Banks applied the Linnaean method to his burgeoning museum collections. From 1772 to 1820, his collectors voyaged to Cape of Good Hope (Francis Masson, James Bowie); West Africa (Mungo Park); the East Indies (Mungo Park); South America (Allan Cunningham); India (Anton Hove); and Australia (David Burton, George Caley, Robert Brown, Allan Cunningham, and George Suttor). David Nelson went on Cook's third voyage (1776–1780) and with Bligh on the "Bounty" (1787–1788). Archibald Menzies collected for Vancouver's North American voyage (1791–1795).

It is not surprising that more than 80 plant species bear his name, including the renowned Proteaceous genus, *Banksia*. His patronage of municipal works and voyages of discovery have ensured that his name also dots maps of Britain, North America, the Pacific islands, and Australia. The latter, as New South Wales, was much influenced by his patronage. Banks was a leading authority and advisor to the British government. In 1779, he recommended Botany Bay for convict settlement. In 1780, he organized surveys by Matthew Flinders, who mapped and named Australia for the first time. Banks communicated with each of the four early governors. Practically everyone who had an interest in early Australia consulted Sir Joseph Banks.

**On risk taking.** . . 1806 (aged 63). Writing to WJ Hooker, then a promising young student who was reluctant to travel. "I was about twenty-three when I began my peregrinations, you are somewhat older, but you may be assured that if I had listened to a multitude of voices that were raised to persuade me I should have been now a quiet country gentleman ignorant of a multitude of things I am now acquainted with and probably never attained higher rank in life but that of a country Justice of the Peace."

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## Cross-references

Cook, James (1728–1779)

## BARBADOS

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## Introduction

Barbados is situated at 13° 10' north, about 150 km east of the Windward Islands of the Lesser Antilles. The island is 32 km long, 23 km broad at its widest dimension, and towards the central interior attains a maximum elevation of 340 m.

Lying just east of the Lesser Antillean volcanic forearc, Barbados is a pinnacle on the broad accretionary prism caused by east-west convergence between the North American and Caribbean plates (Speed and Larue, 1982). The island is composed of a core of deformed Eocene to Neogene marine sediments, exposed in the north-east as the Scotland District, capped by a series of gently buckled reef terraces that record its rapid and differential uplift during the Pleistocene (Taylor and Mann, 1991).

## Pleistocene reef terraces

Fifteen separate Pleistocene reef terraces (Figures 1 and 2) have been identified in this coral cap and represent an episodic record of reef development from 640 ka to 60 ka (Broecker et al., 1968; Mesolella et al., 1969; James et al., 1971; Matthews, 1973; Bender et al., 1979; Edwards et al., 1987; Schellmann and Radtke, 2004). The continuous uplift of the Island at rates of up to 0.5 mm/year have exhumed reefs that correspond to the last six or seven interglacial sea-level highstands, extending as far back as MIS-17 (Shackleton and Matthews, 1977; Fairbanks and Matthews, 1978; Speed and Cheng, 2004). Early advances in radiometric dating of corals established the absolute chronology of these highstand reefs and provided the first confirmation of the Croll–Milankovitch theory of the Quaternary Ice-Age, which holds that orbitally forced variation in northern-hemisphere summer insolation drives changes in ice volume and sea level (Mesolella et al., 1969). Although further improvement in dating precision has subsequently questioned this theory and suggested that deglacial sea-level rise preceded the orbitally forced rise in insolation (Gallup et al., 2002), the precise timing of that rise remains difficult to substantiate due to the subtle diagenetic exchange of U-series nuclides in the fossil corals (Blanchon and Eisenhauer, 2001; Scholz and Mangini, 2007).

## Reef zonation

Aiding the comparison of reef terraces of different ages has been the remarkable stability in their zonation over time, (Mesolella, 1967; James et al., 1971) consisting of:

- A forereef facies of steeply dipping calcarenites and coral rubble, sometimes partially buried by the back reef facies of the next lower and younger terrace.





constitutes lime muds and bioturbated muddy lime sands with isolated colonies of branching corals.

Thickness of these facies varies, determined by the rate of relative sea-level rise at the time of their construction, for example, the *A. palmata* zones can have a vertical thickness of 20 m.

### Diagenesis and caliche

Barbados is an excellent field site for studying diagenesis and caliche formation (Figure 3). In the more arid south and west, aragonite and Mg calcite may be retained in corals

and other organisms for 300 ky (thousand years). In the more humid west, Mg calcite is absent for the 83 ky reefs and aragonite is not found in anything older than 200 ky.

Caliche (calcrete), the product of diagenetic modification at and immediately below the rock-soil/air interface is common on many of the Pleistocene reef terraces of Barbados. The caliche profiles vary from thin, relatively dense, laminated brown micritic crusts to horizons over 1 m in thickness comprising brown micritic stringers subparallel to the surface and cutting through the host structure or substrate (Harrison, 1977; Humphrey, 1997).



**Barbados, Figure 2** The back of the 83,000-year reef terrace with sea stack displaying notch and visor, Barbados (Photo: courtesy, D. Hopley).



**Barbados, Figure 3** A brecciated caliche profile with numerous brown micritic stringers developed in Pleistocene (c. 83,000 yr) limestone on Barbados (Photo: courtesy D. Hopley).

## Submerged reefs

Submerged reefs formed during the post-glacial transgression are also found in Barbados, Macintyre (1967) recognized two offshore ridges that parallel most of the west coast at depths of 15–20 m and 70 m. However, further work quoted in Macintyre et al. (2007a), has shown an impressive series of backstepping of reefs dominated by *A. palmata* starting at depths of about <120 m and flourishing ~19 kya to ~14 kya, which were then stranded by the meltwater pulse 1a when the reef could not keep up with the rate of sea-level rise. A further reef was established to shoreward at a present depth of about –80 m forming 25 m of framework before it too “gave up” in response to meltwater pulse 1b (11.3–11.0 kya). Blanchon and Shaw (1995) identified a further reef at the shelf edge at ca –40 m, which “gave up” ~7.6 kya –6.5 kya in response to a further meltwater pulse. This has been a point of some contention and continued discussion (Blanchon, 2005; Toscano and Macintyre, 2005). While Blanchon has suggested that the composite sea-level curve has been smoothed by incorporating transported clasts, Toscano and Macintyre have justified the lack of a visible “jump” in their curve at about 7.6 ka as being the result of sea level starting to rise above the shelf edge at this time and the resulting “inimical” shelf waters causing the demise of reefs for a short period through sedimentation and eutrophication, rather than a rapid rise in sea level. Factors that need consideration in differentiating between the two arguments include the range with which *A. palmata* can be found (at least 5 m and possibly more on structures such as spurs and grooves) and then extended by storm deposited clasts (>5 m). Also, Barbados’ mean uplift rate of ~34 cm/ka is not steady but irregular in occurrence. Further, the *A. palmata* C<sup>14</sup> dates may not provide an accurate framework for rapid sea-level changes (Toscano and Macintyre, 2003; Bard, 1998). Nonetheless, the reefs of Barbados, both submerged and emerged provide

a source of Quaternary environmental data matched by few places elsewhere. For example, dating of the reefs that developed between each of these jumps also further constrained the offset between the radiocarbon and calendar timescale and were subsequently used to establish a standardized protocol for correcting the radiocarbon ages beyond 10 ka tree-ring record (Bard et al., 1990; Fairbanks et al., 2005).

## *Acropora palmata* demise and the origin of Cobblers Reef

Goreau (1959) was the first to identify the dominant role of *A. palmata* in Caribbean reef zonation. However, concern has been expressed over the widespread loss of this species since the 1980s (see Macintyre et al., 2007a, b, for references). The dominant cause has been white band disease.

*A. palmata* is a dominant component of Pleistocene reefs of Barbados (Figure 4) but as noted initially by Lewis (1960), like elsewhere in the Caribbean there is a distinct paucity of this coral in the modern fringing reefs, although Lewis (1984) later found *A. palmata* was forming the foundation upon which modern reefs were growing. However, more recent studies, especially of Cobblers Reef along the southern shores of Barbados, have led to conflicting interpretations of the evidence for the demise of *A. palmata* on the island.

Cobblers Reef forms a significant bank barrier reef 15 km long on the south-eastern shores of Barbados with a history of vigorous *A. palmata* growth which is now dead, covered by a rich algal growth and sparse living non-acroporid corals (Macintyre et al., 2007b). Dating of *A. palmata* clasts from this reef suggested various storm damage about 4,500 to 3,000 cal years ago with subsequent high energy conditions limiting herbivory and



Barbados, Figure 4 Reef crest *Acropora palmata* in 83,000-year terrace, Barbados (Photo: courtesy D. Hopley).



favoring algal growth, thus limiting the reestablishment of reef framework. A few in situ framework dates are only a few hundred years old, but this late period of growth is believed to have succumbed to high turbidity and eutrophication following clearing for agriculture from the mid 1600s (Macintyre et al., 2007a, b). However, an alternative view has been put forward by Blanchon who believes that hurricane emplacement of older clasts onto the crest of modern reefs, is not valid evidence of the timing of reef demise, which should be established from the age range of in-place colonies from cores through the reef deposit itself. There is the suggestion of a 500–400-year old reef under at least a meter of storm deposit. Such a reef would have grown to about 0.5 m below sea level when covered by storm deposits about 300 years ago. As the reef crest is now 2 m below sea-level, this would require the erosion of ~2.5 m of reef before the storm rubble was deposited. It is possible that both interpretations can be accommodated though not at the high energy Cobblers Reef site. Elsewhere on Barbados in more sheltered locations, reef growth may have continued until European settlement and clearance.

### Hydrogeology (Humphrey, 1997)

The porous and permeable Pleistocene coral cap of Barbados permits ground water recharge where precipitation exceeds evaporation in the higher parts of the island. The Tertiary sediments of the Scotland District provide an aquiclude that prevents downwards movement of water and where this lies above sea level, groundwater flows along the base of the limestones in underground streams. However, towards the coast where the aquiclude lies below sea level, a coastal phreatic freshwater wedge and associated mixing zone are developed. Meteoric vadose, meteoric phreatic and mixing zone waters interact with the young subaerially exposed limestones, resulting in a wide range of diagenetic modification. Barbados provides an excellent source of information for geohydrology and diagenesis in uplifted coral reef environments.

### Conclusion

Reef development in the uplifted and submerged reef terraces and their modern counterparts have yielded an exceptional number of important scientific advances and are a valuable resource that will ensure that Barbados continues to be a focal point for studies of both reefs and quaternary climate change. The past history of study and easy accessibility are two factors that add to this value. Many questions related to, for example, the detailed uplift history of the island still require answers, which may become more precise with advances in dating techniques.

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## Cross-references

Back-Stepping  
 Calcrete/Caliche  
 Diagenesis  
 Eastern Caribbean Coral Reefs  
 Electron Spin Resonance Dating (ESR)  
 Emerged Reefs  
 Huon Peninsula, P.N.G.  
 Last Glacial Interstadials  
 Last Interglacial and Reef Development  
 Meltwater Pulses  
 Postglacial Transgression  
 Sea Level Change and Its Effect on Reef Growth  
 Submerged Reefs

## BARRIER REEF (RIBBON REEF)

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## Definition and introduction

In Battistini et al. (1975), barrier reefs are defined as “a set of coral reefs separated from a non-reefal land by a deep lagoon.” This definition is based on morphology, specifically on the relative position between a land mass (itself not the product of the reef, like a reef island for instance), a lagoon, and a reef. With this definition, an atoll rim is not a barrier reef. Other definitions of barrier reefs are related to their genesis. Darwin (1842) explained their formation by the progressive subsidence of fringing reefs surrounding a volcanic island, slowly creating a lagoon between the barrier reef and the land. After complete disappearance of the island, only barrier reefs remain at the periphery of the system, forming atolls. Thus, atoll rims should also be considered as part of the barrier reef category with this definition. The two types of criteria, modern morphology, and geological genetic processes lead to conflicts. Modern views suggest to first label a reef as a “barrier reef,” according to its modern morphology and configuration within a set of land masses and reef complexes, and then study the local and global genetic geological-scale processes that explain the local barrier-reef morphology.

Ribbon Reefs is a term used to describe the outer shelf reefs of the Northern Great Barrier Reef, from 15° S off Cooktown up to 10° S in the Torres Strait. They are sequentially named by numbers (Ribbon Reef No 1, Ribbon Reef No 2, etc.). By similarity, the term has been applied to linear, long, winding reefs, including atoll rims and large banks, but it is not of common use.

Although demonstrated by deep coring projects into Pacific Ocean atolls (Mururoa atoll), the Darwinian fringing-barrier-atoll genetic succession can be applied to only a limited number of oceanic configurations worldwide. Instead, the role of a number of factors need to be taken into account: subsidence, antecedent substrate available for Holocene coral colonization and growth, eustatic sea-level variations, freshwater dissolution during the period of emergence at low-sea stands, and local tectonic processes are often necessary to explain the modern morphology. The relative importance of these factors is still debated to explain barrier reef morphology (Purdy and Winterer, 2006).

## Morphology

Classification of reefs using their planar, view-from-above, morphology as indicators of their genesis is common practice. In a barrier reef context, Hopley (1982) discussed for the Great Barrier Reef the validity of the

previous classifications obtained from the interpretation of aerial photography, but he accounted for new data from coring and from recent advances in understanding reef growth. He showed that previous interpretations could be misleading to infer a reef-growth development typology. Then, Hopley (1982) established a new classification for the shelf reef of the Great Barrier Reef, including as a specific zone the northern Ribbon Reefs, which display a typical barrier morphology, with linear reefs parallel to the continent, from 15° S up to 10° S in the Torres Strait. South of Cooktown, the Great Barrier Reef consists of a dense (e.g., the Swains group) to open matrix (e.g., the Capricorn Bunker group) of shelf patch reefs, also called platform reefs. The size of these patch reefs displays a wide range, from a few hundreds of square meters to several tens of square kilometers. The unique and photogenic Pompey Group, at 21° S displays a general barrier linear morphology, with very large individual reefs characterized by subsurface karstic formations, blue holes, and numerous deep and narrow channels.

Recently, remote sensing technology provided complete coverage of reefs worldwide using high spatial resolution Landsat satellite images (Andréfouët et al., 2006a). This new data set allows examining in details all barrier reefs worldwide. A detailed typology was inferred, although it cannot be precisely coupled in most locations with coring data to relate planar morphology with genetic processes like in Hopley (1982). Thus far, this link has been done only for New Caledonia (Andréfouët et al., 2009a). Nevertheless, the diversity of morphologies are potential indicators of local processes keeping in mind the same caveats that Hopley (1982) put forth for the interpretation of Great Barrier Reef structures.

Landsat images suggested a hierarchical typology that can be applied to oceanic and continental reefs. In this typology, atolls are described separately, and thus atoll rims are not considered like barrier reefs. First, two main types of barrier reefs are distinguished on the top of the hierarchy: the outer shelf and intra-shelf barrier. The intra-shelf barrier is composed of continuous lines of reefs in a lagoon, well separated from the outer shelf barrier. Then, these two types of barrier reefs can themselves be separated into barrier, multiple-barrier, faro-barrier, imbricated-barrier, coastal-barrier, and fringing-barrier types. Multiple-barriers are made of series of parallel reef flats developed close to each other and sometimes connected together (see Guilcher, 1988). A faro-barrier is a structure made of faros, or in other words a series of reefs with a central enclosed lagoon. An imbricated-barrier is a section of barrier, which is turning around itself, the outer side turning to the inner side when bending, thus changing completely the degree of exposure and the types of habitats. An imbricated-barrier can also be a barrier that terminates in the lagoon of a second separate barrier. A coastal-barrier is an intermediate configuration between a barrier and a fringing reef, that is, there is no deep lagoon, but a shallow sedimentary terrace that clearly separates outer reef flat habitats from fringing-like habitats.

A fringing-barrier is a section of barrier that harbors large islands, thus displaying fringing-type habitats in an outer barrier environment. Examples of all these barrier reef types are given in Figure 1. These types describe the diversity of barrier reefs worldwide based on their morphology visible on remote-sensing images.

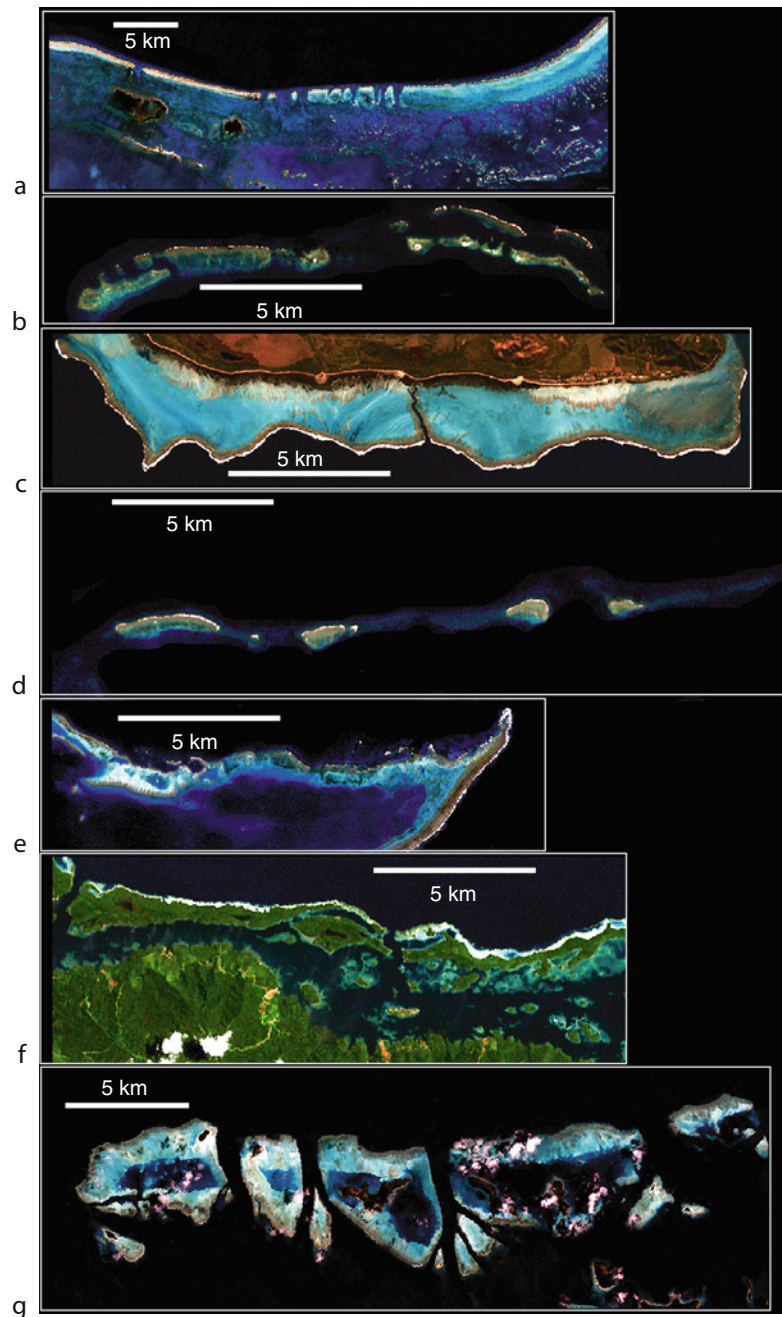
## Locations

Beside the Australian Great Barrier Reef discussed above, barrier reefs are found in all coral reef provinces worldwide. In the Caribbean Seas and Atlantic Ocean, the longest system is offshore Belize, approximately 200 km long (Figure 1). This Belizean section is actually the only true outer barrier system of the so-called Meso-American Barrier Reef System (Mexican Yucatan, Belize, Guatemala and Honduras), which includes fringing reefs for most of its length. Honduras Bay Islands include a drowned barrier structure and narrow coastal barrier systems. In the Bahamas, Andros Island is often cited as having one of the longest barriers in the Caribbean-Atlantic region, or even in the world, but it is a fringing and coastal barrier system, without any deep lagoon. Other small barrier systems are found in Caribbean Panama, Columbian Islands (e.g., Providence Island), Venezuela (Los Roques), Greater Antilles (especially Cuba, but also Haiti and Dominican Republic) and Lesser Antilles (e.g., Guadeloupe), and in the Bahamas (e.g., north of Little Bahama Bank).

In the Indian Ocean, the longest system is a nearly 1,000 km long drowned structure along the west coast of Madagascar, at the edge of the shelf. It is poorly documented, and was absent in the region coral reef maps until recently (Andréfouët et al., 2009b), although it is visible in marine charts of this area. Southwest Madagascar (the Toliara region), Mayotte Island, and on the other side of the Mozambique channel, Mozambique, Kenya, and Tanzania (e.g., the Tanga area) have small sections of barrier reefs, including coastal barrier systems. Barrier reefs occur in Mauritius Island at various stages of development (Montaggioni, 2005). The large outer Seychelles plateau, also a deep subtidal system, present a barrier-like peripheral structure formed by large deep, drowned, platforms intersected by deep passes. In the Eastern Indian Ocean, the west coast of Australia displays the Ningaloo Reef system. It is generally described as a fringing reef, but its structure and habitat zonations are consistent with the definition of a coastal barrier reef.

The Red Sea has unique reef morphologies (Purkis, et al., 2010), and several areas can be classified as barrier reefs especially in Saudi Arabia (e.g., Al Wadj Bank area), Egypt (tip of the Sinai Peninsula), and South Sudan. Most of the Red Sea is bordered by fringing structures, which for the widest show coastal barrier like-patterns.

Southeast Asia (especially in the Philippines and Indonesia), including Japan (Ryukyus Archipelago) display numerous significant barrier reefs at various stage of development (e.g., Spermonde Barrier Reef), from coastal to outer barrier reefs, including drowned ones (e.g., east of



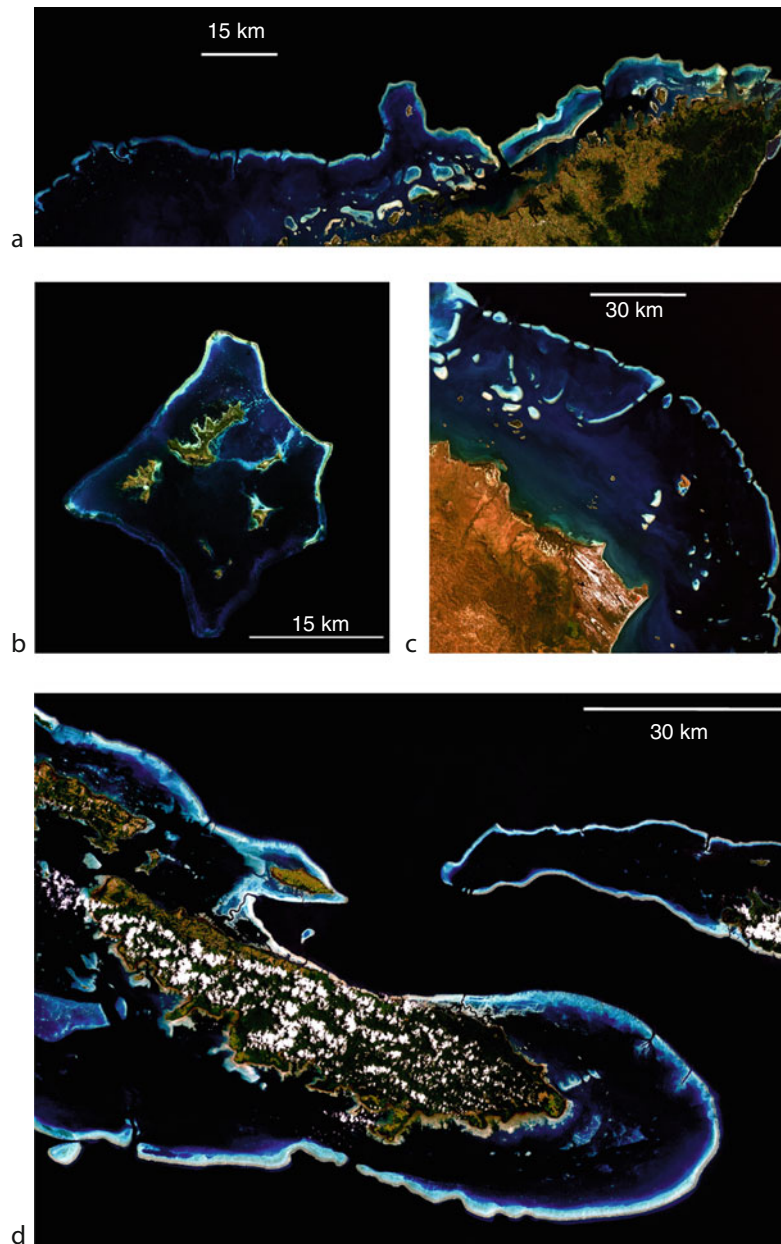
**Barrier Reef (Ribbon Reef), Figure 1** Examples of outer barrier reef morphologies captured with the Landsat 7 spaceborne sensor. All images have been rotated for a better comparison. Scales are different. (a) A section of the Belize barrier reef with a narrow intertidal reef flat, (b) a double barrier reef on the east coast of New Caledonia, (c) a coastal barrier reef on the West Coast of New Caledonia, (d) a partly drowned, partly intertidal barrier reef on the southeast coast of New Caledonia, (e) an imbricated barrier reef on the southwest coast of New Caledonia; differences between reef flat structures when the reef is bending are evidenced in this example, (f) a fringing-barrier reef in New Georgia, Solomon Islands, (g) a faro-barrier reef, on the west side of Suddest Island, in eastern Papua New Guinea.

the Aceh province of Indonesia). Most of these Asian reefs remain poorly studied (Tomascik et al., 1997).

The home of the most significant barrier reefs is the Western Pacific (Figure 2). Besides the Ribbon Reefs of

the Great Barrier Reef, which span 1,200 km, New Caledonia is surrounded by an intertidal 1,300 km long barrier that includes a large variety of morphologies (Figure 1). The Eastern region of Papua New Guinea, also harbor





**Barrier Reef (Ribbon Reef), Figure 2** Examples of Pacific Ocean barrier reefs captured with the Landsat 7 spaceborne sensor. (a) A section of the Great Sea Reef north of Vanua Levu, Fiji. (b) The barrier reef, partly intertidal, partly drowned that surrounds Mangareva Island in southeast French Polynesia. (c) A section of the Ribbon Reefs in the north of the Great Barrier Reef, Australia. (d) A section of the Calvados Barrier Reef in eastern Papua New Guinea.

from Port Moresby (Papuan Barrier Reef, partly drowned) to the tip of the Archipel de la Louisiade (Calvados Barrier Reef, a 570 km long reef around Suddest Island), an uninterrupted stretch of morphologically diverse barrier reefs (Andréfouët et al., 2006b). This region also includes faro-barrier reefs (Figure 1). Other spectacular Pacific Ocean barrier reefs are the Fijian Great Sea Reef in the north of Vanua Levu Island (410 km) and the barrier reefs surrounding Palau Island (390 km). Pacific Islands from

Micronesia, Melanesia, and Polynesia display many barrier reefs of few tens of kilometers long, some that can be typically Darwinian (e.g., Bora Bora or Mangareva in French Polynesia, Aitutaki in the Cook Islands).

#### Drilling in barrier reefs

Only a few cores have been retrieved from the large barrier reef tracts, including in New Caledonia (Coudray, 1976;

Cabioch et al., 2008), Belize (Gischler et al., 2000, 2010; Purdy et al., 2003; Mazzullo, 2006), and the Australian Great Barrier Reef (Alexander et al., 2001; Webster and Davies, 2003; Braithwaite et al., 2004; Hopley et al., 2007).

Coring analyses of the barrier reef tract around New Caledonia revealed the interplay between margin subsidence and eustatic sea-level variations. Combination of lithological and paleoecological descriptions, Uranium dating methods, magnetostratigraphy, and nannofossil-based biostratigraphy document the role of both global climate and regional tectonic history on the reef initiation and growth of the barrier reef. Several successive lithological units were evidenced formed during the high sea stands of the interglacial periods. It appears that the period ranging over the last 400 ka (1 ka = 1,000 years) was probably the period of optimal conditions to explain the luxuriant reef expansion in New Caledonia over this epoch (Flamand et al., 2008; Cabioch et al., 2008).

In French Polynesia, the Tahiti barrier reef was cored to analyze the history of its development during the last deglacial sea-level rise (i.e., the last 20 ka, 1 ka = 1,000 years). The first cores made in the 1990s revealed a continuous reef growth from 14 to 6 ka from 90 m to the reef surface (Bard et al., 1996; Montaggioni et al., 1997). More recently, the Integrated Ocean Drilling Program (IODP) drilled the Tahiti barrier reef in three sites to investigate reef development during the last deglacial sea-level rise, and the evolution of the sea surface temperature during the last deglaciation (Camoin et al., 2007).

The Belize barrier reef is another well-studied reef, but only with short cores that document the Holocene and late interglacial period of growth. Additional seismic and lithological data provide information on the tectonic and eustatic controls on the Belize barrier reef development (Mazzullo, 2006).

The Great Barrier Reef internal Pleistocene structure remains poorly known. Davies and Peederman (1998), Alexander et al. (2001), Webster and Davies (2003), Braithwaite et al. (2004), and Braithwaite and Montaggioni (2009) report limited deep coring data given the extent of the system (see *Great Barrier Reef: Origin, Evolution, and Modern Development*). The most recent studies suggest that the Ribbon Reef No 5 was initiated 770 ka ago, followed by Pleistocene repetitive period of reef development and erosion with ten identified depositional units, despite major fluctuations on sea level and perhaps climate. IODP ongoing drilling (February–March 2010) should provide new information in the near future on the development of the Ribbon Reefs in particular, and for several other inner shelf locations as well.

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## Cross-references

[Belize Barrier and Atoll Reefs](#)  
[Darwin, Charles \(1809–1882\)](#)  
[Double and Triple Reef Fronts](#)  
[Forereef/Reef Front](#)  
[Great Barrier Reef Committee](#)  
[Mururoa Atoll](#)  
[New Caledonia](#)  
[Reef Typology](#)  
[Remote Sensing](#)  
[Sea Level Change and Its Effect on Reef Growth](#)  
[Subsidence Hypothesis of Reef Development](#)

## BASSETT EDGES

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## Synonyms

[Bassett edges](#); Exposed edge of strata inclined upward; Outcrop; Strike ridges.

## Definition

Bassett edges are outcrops of inclined beds, forming a jagged surface of low irregular projections resulting from differential erosion of often steeply dipping layers

of lithified coral shingle, with a bed thickness of a few centimeters and relative relief of 2–3 dm.

A bassett is an old term used by miners in the 18th and 19th centuries to describe the emergence of subsurface geological strata at the ground surface. “Bassett edges” was introduced into the modern reef literature by J. Alfred Steers (*Steers, James Alfred (1899–1987)*) to describe the lower cemented vestiges of coral shingle ramparts on Australia's Great Barrier Reef, where “the separate beds are often truncated and the bassett edges rise up” (*Steers, 1929*).

What Steers found particularly interesting was the dip of the beds, which was “very often landward,” implying “that the rest of the spit or ridge of shingle formerly existed to the windward of the present outcrop.” Thus, the presence of low strike ridges that dip away from the reef front preserve the remains of old shingle rampart systems that have subsequently been eroded.

A more formal description and explanation of bassett edges on reefs of the northern Great Barrier Reef was given by Scoffin and McLean (*1978*). They found that (1) the inclined bedding of bassett edges represent the cemented foreset layers of the leading edge of shingle ramparts; (2) the irregular projections result from differential erosion related to subtle differences in the degree of cementation and constituent texture; (3) cements are typically a chalky micrite of high magnesium calcite; (4) bedding occurs as steeply dipping foresets (40–70°) on tongue shapes, like anticlines plunging to leeward, and as shallowly dipping (20–40°) arcuate bands between; (5) the inner buried portions of ramparts have to remain stationary for some time to allow lithification; and that is why (6) bassett edges are commonly found on the central and inner parts of a reef flat rather than toward the outer edge where wave action continually mobilizes rampart rubble.

Though the cemented foreset beds of shingle ramparts are not restricted to the Great Barrier Reef, the term bassett edges is not in common use in other reef areas.

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## Cross-references

[Boulder Zone/Ramparts](#)  
[Platforms \(Cemented\)](#)

## BEACH ROCK

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## Synonyms

[Beach rock](#); Beach sandstone



## Definition

Beach rock results from lithification of unconsolidated sediments by calcium carbonate cements in the tidal zone of mainly tropical and subtropical beaches. Aragonite and calcite, in a number of crystalline forms, are the primary agents of cementation. All kinds of beach sediments can be cemented, from fine sands to gravels of biogenic and/or terrigenous origin. Beach rocks can also vary greatly in texture and degree of lithification, some being quite porous and friable, others being dense and highly indurated. Beach rock takes on the disposition of the parent beach, including the preservation of beach slopes and stratigraphy. Outcrops usually show a number of distinct bands that represent the bedding planes, internal laminae, and sedimentary structures preserved during the cementing process which can be quite rapid.

## Description

Beach rocks are a common and conspicuous feature of many island and mainland shores in reefal areas. They vary from small discontinuous exposures of cemented sediments to extensive outcrops tens of meters wide and hundreds of meters long. More normally, beach rock occurs as narrow elongate strips, 5–20 m wide and 100–200 m long, comprising an overlapping sequence of separate bands with a definite seaward dip varying from 5 to 15°. The thickness of individual bands is usually around 0.1–0.2 m with the total thickness of outcrops ranging from 0.5 m to more than 2.5 m, being thickest in areas of high tidal range. Banding is often associated with textural bedding, while the seaward dipping layers are characteristic of foreshore sedimentation. Different lithofacies have been recognized both in the vertical and within a single band.

Beach rocks generally occur in the swash zone of a beach and frequently mobile sand or gravel obscures the upper and/or lower portion of an outcrop. Temporary burial and exposure of formations may result from seasonal deposition and erosion of local beach sediments, or from alternating storm and fair weather regimes. Relic beach rocks may be found either landward, or more commonly, seaward of the present beach.

Beach rock is not the only cemented rock on coral coasts and reef islands. Others include conglomerates (*Conglomerates*), cemented platforms (*Platforms Cemented*), phosphate rock, *Eolianite*, and cay sandstone or cay rock, the last often being confused with beach rock *sensu stricto*, although the distinction between beach rock and cay rock is made quite clear by Gischler and Lomando (1997).

## Distribution

In a recent review Voudoukas et al. (2007) note that, until the early 1960s, the prevailing opinion had been that beach rock formation, involving carbonate cements, was primarily limited to tropical and subtropical coasts. However, subsequent observations have shown beach rock is

also present on temperate and higher latitude coasts with individual occurrences reported from South Africa and New Zealand in the southern hemisphere and Japan and Scotland in the northern hemisphere. Nevertheless, the great majority of beach rocks are found in low latitude locations, although there are particularly extensive outcrops around the Mediterranean Sea. Microtidal coasts tend to be favored, although there are many outcrops along island shores in areas of high tidal range such as in the central and southern Great Barrier Reef, Australia where tidal ranges of 2.5–8 m occur. There, and in other reef areas, beach rock is mainly associated with calcium carbonate beaches, and on coral atolls beach rock (*Beach Rock*) is generally the most common and obvious “rock” apart from biohermal reef rock.

## Grain size and composition

The grain size and composition of beach rock reflect that of the parent beach at the time of cementation. On coral reef coasts, beach rocks classically comprise a mix of sand- to gravel-sized sediments made up of the skeletal remains of calcareous organisms such as mollusks, benthonic foraminifera, coralline algae, and *Halimeda*, particularly in the sand to pebble size fraction. The coarsest components are frequently whole or fragmented coral clasts, especially of branching and foliaceous corals, and smaller massive corals as well as reworked fragments of reef rock and pieces of beach rock. There are also occurrences of beach rocks whose component grains are noncarbonate; volcanoclastic grains are common on volcanic islands, and quartzose sediments on rocky continental coasts. Many beach rocks also contain “erratic” materials, including exotic ballast rocks and even human artifacts and litter ranging from ancient pottery fragments to articles of war and modern beer cans and bottle glass.

## Cements

*Aragonite* and *Calcite* and especially high magnesium calcite are the predominant cementing agents of beach rocks. Both minerals are dimorphous with the same chemical composition (calcium carbonate) but different crystal shape and symmetry; aragonite is orthorhombic, and calcite is trigonal. Thin section microscope and scanning electron microscope images of beach rock cements reveal a wide range of morphologies and fabrics. Three common morphologies in tropical beach rocks were described by Scoffin and Stoddart (1983) as: micritic coatings of either aragonite or calcite on parent grains; fibrous or bladed crusts of elongate crystals commonly as aragonite; and classical equant crusts associated with magnesium calcite. They also described three common cement fabrics: isopachous fringes of uniform coatings around grains; meniscus cements; and gravitational or pendant cements. None of these fabrics are pore filling.

Voudoukas et al. (2007) suggest that well-cemented beach rocks may have undergone several diagenetic phases, each one producing cements of a different

mineralogy and habit. In sequence, beach rock cementation may commence with the precipitation of micritic cements around in situ grains, followed by the precipitation of prismatic crystal rinds, and finally pore filling, peloidal, spar, and infiltrating micrite cements. Changes to the nature and characteristics of cement types can also take place. Relic beach rock cements may show evidence of dissolution and/or recrystallization. A beautifully illustrated and described chronosequence of carbonate fabrics in 52 beach rock samples from the northeastern Mediterranean is presented in Desruelles et al. (2009).

### Origin of cement

While earlier descriptions exist of beach rock, including those of Darwin (*Darwin, Charles (1809–1882)*) and Dana (*Dana, James Dwight (1813–1895)*), the first detailed mineralogical and chemical analyses were carried out on samples from *Funafuti Atoll* collected during the Coral Boring Expeditions from 1896 to 1898. These analyses, together with thin section examination of several “calcareous sandstones” reported by David and Sweet (1904: 73–74), “shows the cement to be a fibrous radial calcite” and that the beach sandstones formed through the evaporation of calcium carbonate-charged fresh water oozing through an island’s intertidal beach sands, where “calcium carbonate would form and be deposited as cement between the sandy particles.” While there have been subsequent advocates of this fresh water lithification process, several other mechanisms have been proposed including: physicochemical precipitation from evaporating sea water or mixtures of meteoric water and sea water; the escape of CO<sub>2</sub> or degassing from groundwaters saturated with carbonates; and precipitation directly or indirectly through biological activity, especially by microbial cements (Khadkikar and Rajshekhar, 2003).

Detailed descriptions and illustrations of the range beach rock cements as well as modes of beach rock formation are summarized in a series of excellent reviews over the last several decades by Stoddart and Cann (1965) in the 1960s, Davies and Kinsey (1973) in the 1970s, Scoffin and Stoddart (1983) in the 1980s, Gischler and Lomando (1997) in the 1990s, and most recently by Voudoukas et al. (2007). These contributions provide episodic snapshots of the status of on-going beach rock research and its developments, especially related to the origin of beach rock. While beach rock origin has been the main matter of discussion over a long period of time, it is now quite clear that there is no one unique mechanism that results in the formation of beach rock, nor any exclusive set of environmental factors that control cementation.

Rather, beach rock formation is multigenetic, with a number of inorganic and organic formative processes, including direct cement precipitation from marine or fresh or mixed marine and meteoric waters, and cementation from biological processes notably microbial (fungi and bacteria) activity. Similarly, a range of factors appear to control cementation, including interstitial water

temperature, pH and salinity, through-flow and tide-level variations, the presence of calcium carbonate, organic compounds and microbes, as well as the stability of beach sediments, or as Gardiner (1903: 342) put it so quaintly “where the beach is at rest so far as growth outwards is concerned.” This list of factors is not exclusive, nor is their relative importance known for any beach rock site.

### Speed of cementation

Cementation can take place rapidly on time scales of a few years. Examples are provided by the incorporation of WWII relics into beach rocks on several islands across the Pacific and on the northern Great Barrier Reef. Gardiner (*Gardiner, John Stanley (1872–1946)*) reports on the removal of beach rock slabs for gravestones and building materials on the Fijian island of Rotuma and throughout the *Maldives* and their replacement by newly cemented or case hardened bands in a few months in the same location, suggesting a sustainability in local quarrying of beach rock. But perhaps the most famous example of beach rock formation is that reported in 1924 by Reginald Daly (*Daly, Reginald Aldworth (1871–1957)*) from the Tortugas Marine Laboratory, where within 2 years of the 1910 storm depositing a fresh ridge of loose calcareous sand in the vicinity of the laboratory, the deposit had been lithified to a depth of about 0.75 m, forming a band of typical beach rock.

### Age of beach rock and problems of dating

Beach rock cements are clearly younger than the grains and clasts that make up the bulk of the rock. Moreover, in reefal areas both the sediment and cement are composed of calcium carbonate. Thus, dating of whole-rock samples is problematical and will give ages based on the relative proportions of the original skeletal components and secondary cements, both of which are likely to be quite variable. Constituent clasts may be dated to obtain a maximum age, but to get an age closer to the time of beach rock formation, the cement must be dated. Obtaining an adequate amount of uncontaminated cement is challenging, and there is always the possibility of multigenerational cementation and recrystallization. However, Desruelles et al. (2009) report on successfully extracting micrite cements from beach rock at two sites in Turkey and obtaining AMS dates for these cements.

Voudoukas et al. (2007) include the estimated age of exposed beach rocks from 20 locations around the world, only six of which are from modern coral reef areas. They believe that the majority of dated beach rocks are fossil forms, 1,000–5,000 years old, but admit that the abundance of recent beach rocks is likely to be underestimated.

In spite of a large and increasing number of radiometric dates from beach rock samples around the world, those from modern coral reef areas have had limited success in dating the time of formation. For example, corrected radiocarbon dates of five whole-rock and one shell sample

from beach rock on six cays in Belize range from AD 345 to 1435, although Gischler and Lomando (1997) note that these may not be reliable ages and should only be taken as an approximation. On the Great Barrier Reef, Chivas et al. (1986) extracted nine firmly cemented clam shells (*Tridacna*) from low intertidal beach rock at Lady Elliot Island. The beach rock was known to have formed during the twentieth century, although two of the three nonmodern clams had conventional radiocarbon ages of 1830 and 6540 yBP, indicating millennial scale reworking of these well-worn shells.

While still in its infancy, optically stimulated luminescence (OSL) and thermoluminescence (TL) dating on feldspar and quartz grains from beach rocks in northeastern Brazil has been carried out (Tatumi et al., 2003). This technique has limited potential in most coral reef areas where both beach rock components and cements comprise calcium carbonate.

### Morphodynamics and shoreline change

Beach rock formation alters the nature of the shoreline, and turns what was once a mobile beach into a rocky shore. In so doing the permeable character of the beach is changed to an impermeable barrier that precludes swash infiltration and inhibits seaward groundwater flows. Two effects of these changes can be noted. First, the impermeable ramp does not reduce swash uprush and backwash, and may result in run-up reaching higher levels than previously causing overtopping of the beach rock and scour behind it. Second, the impeded groundwater outflow is redirected to the sides and base of the outcrop which together with wave, current, and tidal actions can result in lateral erosion and undermining of outcrops. Thus, paradoxically, while beach rock can be an effective natural beach defense, equivalent to a revetment, like many other shore protection structures, edge effects can result in basal undercutting and lateral erosion. Evidence of the former is often expressed in cracks and fractures, sometimes in attractive tessellated patterns, as well as subsidence of beach rock bands and slabs. Evidence of the latter can include landward offset of the waterline and retreat of the nearby beach. The presence of beach rock also has a significant ecological impact, as surficial and interstitial flora and fauna of the mobile beach is replaced by assemblages of benthic organisms on beach rock substrate.

Beach rock, as a consolidated rock, provides an excellent marker of the actual shore position when it formed. Persistence of the “frozen beach” (Caldas et al., 2006) is dependent on the sediment budget for that shoreline sector. A positive budget can result in accretion, burying the outcrop landward of the new shore. A negative budget can result in beach erosion, isolating the beach rock outcrop to seaward. This latter scenario seems especially common on reef coasts and reef islands, where one or more lines of beach rock extend offshore. While outcrops parallel to the present shore are most common, some

amazing strandline patterns can be found. On atolls, lagoonward migration of reef islands is a common feature. In addition to leaving a trail of beach rock to seaward, continued lagoonward migration may ultimately expose lagoonward dipping beach rock (from the former lagoon shore) on the seaward beach. There are several examples of this on modern reef islands, although the best historical descriptions are from the Maldives (Gardiner, 1903) and Funafuti atoll (David and Sweet, 1904).

### Beach rock as a sea-level indicator

Not only can fossil beach rock be used to provide evidence of planimetric shoreline change, but because its vertical range is restricted to between tide marks, its value for paleo-sea level studies has long been recognized. Hopley (1986) has provided the most definitive study of beach rock as a sea-level marker, indicating its pros and cons. He concludes that it is not particularly reliable because the exact upper limit of formation is poorly constrained. Indeed, Kelletat (2006) has argued that the large vertical extent in some beach rock occurrences in microtidal locations may be ascribed to cementation in the supratidal zone, although this has been vigorously disputed (Knight, 2007).

Notwithstanding these reservations, relic beach rock is still seen as an important paleo-sea level marker, although rarely as the sole indicator. In reefal areas emphasis has been on detecting mid-late Holocene changes in sea level and specifically to identify whether or not there has been a sea-level high stand. Elevations of relic beach rock have contributed to confirming a sea level higher than present on *Cocos (Keeling) Islands*, the northern Great Barrier Reef, Cook Islands, French Polynesia, and elsewhere in the Pacific. Beyond the major reef areas, beach rock has also been used to develop more continuous sea-level histories, such as in northeast Brazil (*Brazil, Coral Reefs*) where beach rock elevations and AMS dating of mollusk fragments from 12 samples suggest that sea level was at  $-3$  m 7000 cal yBP, reached  $+1.3$  m about 5900 cal yBP, after which it fell in linear fashion to its present position (Caldas et al., 2006). And, on the Sardinia–Corsica coast in the Mediterranean numerous beach rock outcrops have been preserved along the shorelines and at different depths on the continental shelf down to  $-29$  m. These have been dated from 9705 to 180 (cal yBP) enabling Lambeck et al. (2004) to derive a detailed local sea-level history over the last 10,000 years.

### Surface features and beach rock erosion

Beach rock is a striking feature of coral reef coasts and reef islands. The contrast between fresh light-colored biogenic sands and darker beach rock outcrops is often quite stark. Most observers note the inclined, banded nature of intertidal outcrops, their low-relative relief and bare surfaces. In detail, however, beach rock surfaces are rarely bare, except where the substrate is being constantly scrubbed



by sediment-laden swash. Typically, there is a shore-parallel zonation of both morphological forms and biological organisms, the zonation frequently being expressed in different surface colors representing pigments of various microbial communities including cyanobacteria, algae, and fungi that inhabit the beach rock. Diez et al. (2007) show such communities can be dominated by cyanobacteria that fix nitrogen at night, and constitute important primary producers that provide the base of the intertidal and nearshore food webs.

Bioerosional agents including fish, echinoderms, worms, and mollusks feed on the microbial mats, and at the same time, scrape, bore, and burrow into the beach rock as do some of the blue-green algae (*Algae, Blue-Green Boring*). Many biolithophagic organisms produce distinctive micromorphological features such as boreholes, burrows, and tunnels, while others leave smaller traces like homing scars from limpets and tooth marks from parrot fish. The geological significance of bioerosion of beach rock was recognized several decades ago (McLean, 1974) and the rates and impact of a number of beach rock eroding taxa, including echinoderms and chitons continue to be investigated (e.g., Barbosa et al., 2008).

Kelletat (2006) has noted that many beach rocks are in a state of destruction. Mechanical erosion and abrasion of beach rock can result in smooth surfaces, as alluded to above, and to the development of rhythmic transverse furrows or grooves in the lower tidal zone, and potholes in the upper tidal zone. Other common features include undercuts, notches, fractures, and broken slabs caused by basal undermining, marginal scour, and breakage due to mechanical strain and weakness. In places, where beach rock outcrops have been exposed for a long time, upper surfaces often show a jagged pool and pinnacle topography or microkarst resulting from a combination of solution processes (*Solution Processes/Reef Erosion*) and *Bioerosion*.

Destruction of beach rock can also be the result of human activity, where outcrops are quarried like slates and used as paving stones, building and fencing materials and tombstones. Such usage is especially true on reef islands in atoll states where solid rock is sparse.

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## Cross-references

[Algae, Blue-Green Boring](#)  
[Aragonite](#)  
[Bioerosion](#)  
[Calcite](#)  
[Conglomerates](#)  
[Eolianite](#)  
[Micrite](#)  
[Phosphatic Cay Sandstone](#)

## BELIZE BARRIER AND ATOLL REEFS

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### Definition

The Belize barrier and atoll reefs form the largest modern reef system in the Atlantic Ocean. Belize, formerly British Honduras, is located in a subtropical climate with air temperatures from 25 to 29°C and water temperatures that range from 24 to 32°C on average (Wantland and Pusey, 1975). Trade winds blow from the east and northeast for most of the year. Climate is also influenced by the position of the intertropical convergence zone (ITCZ), which is positioned over Belize in the summer–fall causing elevated rainfall. The ITCZ moves to the south in winter–spring, which results in lower precipitation rates. Rainfall rates on the mainland increase from 150 cm/year in the north to >400 cm/year in the mountainous south. Belize is a microtidal area with a tidal range of <0.3 m. Major hurricanes have repeatedly hit Belize and are a major factor of reef development and disturbance (Stoddart, 1963). In 1998, a combination of a major hurricane and an extensive bleaching event led to a significant loss of live coral cover in the Belize reefs (Mumby, 1999; McField, 2000).

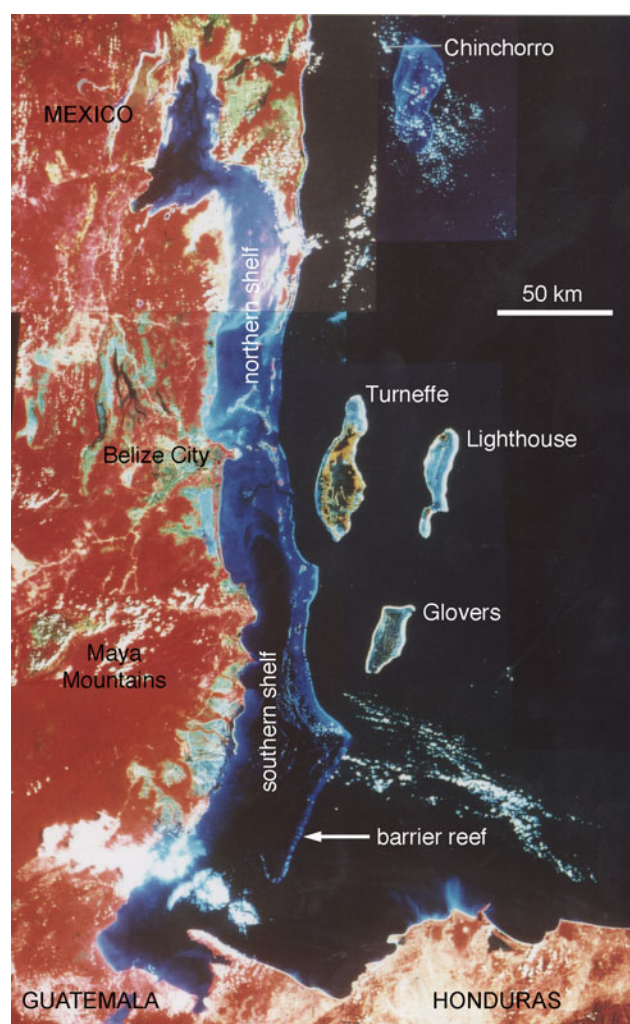
### Geomorphology

The Belize Barrier Reef is about 250 km long and almost continuous (Figure 1). It is located at the shelf margin. The distance to the coast increases from 25 km in the north to 50 km in the south. Likewise, water depth on the shelf increases from max. 5 to 50 m in the same direction (Figure 2). At the southern end, the reef forms a peculiar hook-shaped morphology. In the north, towards the Mexican (eastern Yucatan) coast, the barrier reef shelf margin transitions into a fringing reef. On the Belize shelf, thousands of coral patch reefs may be found. There are also small shelf atolls, some of which have characteristic rhomboid shapes (Figure 3). Fringing reefs are rare adjacent to the northern inner shelf coast; however, isolated nearshore reefs do occur on the southern shelf that is influenced by siliciclastic input. This is a curious observation, because it is contrary to common belief that coastal reefs should flourish and be abundant in carbonate rather than siliciclastic environments. The three offshore atolls vary in size from 200 to 525 km<sup>2</sup> (Stoddart, 1962; Gischler and Lomando, 1999). Glovers Reef has a typical atoll morphology with an almost continuous marginal reef enclosing an 18-m-deep lagoon. The lagoons of Lighthouse Reef and Turneffe Islands are only 6–8 m deep. The Turneffe lagoon is restricted due to a dense rim of mangroves; corals are rare and *Halimeda* occurs in great abundance. Both on the shelf and the atolls, hundreds of small islands occur, including sand islands, rubble islands,

mangrove islands, and combinations of these, which are locally called cays (Stoddart, 1965).

### Organisms and reef zonation

A large variety of corals, algae, mollusks, crustaceans, echinoderm, fish, and other reef-related organisms have been described from the Belize reefs. An excellent overview was given by Rützler and Macintyre (1982), based on quantitative studies conducted along a transect across the central barrier reef near Carrie Bow Cay, the location of the Smithsonian field station. Forty-eight stony coral species have been described. The most important reef-building corals include the branched *Acropora palmata*, the foliaceous *Agaricia* sp., and the hydrocoral *Millepora* sp. that predominate in forereef areas. Massive corals of the *Montastraea annularis* group may be found both in forereef and lagoonal or outer shelf regions. *Acropora cervicornis* used to be very common in backreef, lagoonal,



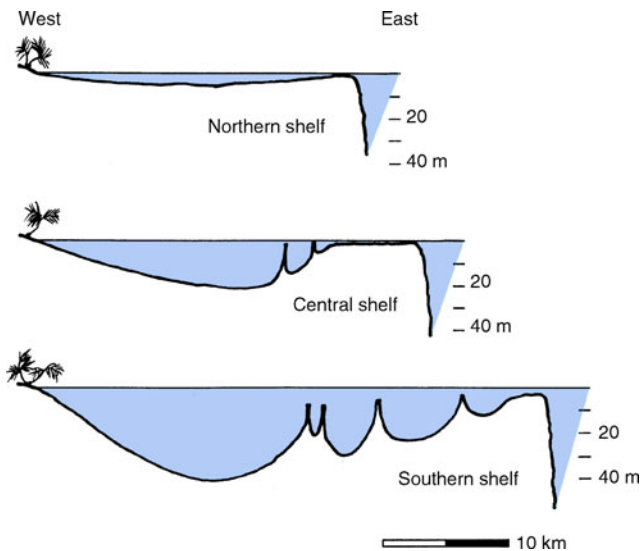
**Belize Barrier and Atoll Reefs, Figure 1** Satellite image of the Belize reef system. Barrier reef is 250 km long.

and shelf areas; however, it was significantly decimated by disease in recent years (Aronson and Precht, 1997). Coastal reefs and restricted lagoons are dominated by the tolerant *Siderastrea siderea*. Stoddart (1962), James et al. (1976), James and Ginsburg (1979), and Macintyre et al. (1987) defined zones in marginal reefs of Belize, largely based on the occurrence of corals and other invertebrates and algae and based on submarine topography (Figure 4). James and Ginsburg (1979) described the deep foreereef of Belize barrier and atoll reefs based on

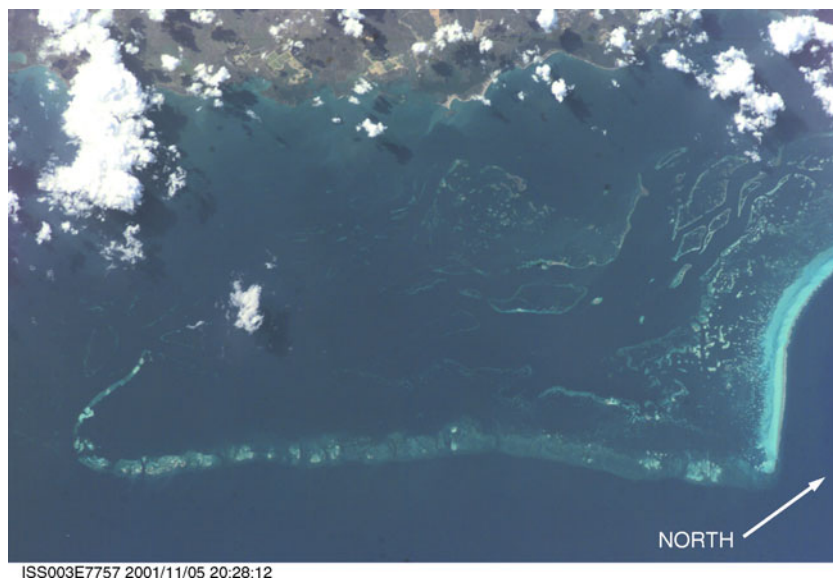
submersible observations. At the base of the sloping foreereef in 15–40 m depth, they discovered a steep drop-off leading to an almost vertical wall that reaches down to 100–150 m depth. At the base of the wall, a sediment slope with rubble and larger blocks may be found.

### Sediments

The Belize shelf is a classic example of a mixed carbonate–siliciclastic system (Figure 5). Siliciclastics originating from the southern mainland (Maya Mountains) and carbonate largely produced on the outer shelf mix on the inner shelf to form marl. Purdy (1974) elaborated the first systematic sediment map of the Belize offshore area. Gischler and Lomando (1999) detailed sediment types on the offshore atolls. A compilation of existing data including a detailed sediment map covering the entire Belize offshore area may be found in Purdy and Gischler (2003). Eleven facies may be delineated on the Belize shelf and atolls, with corals, coralline algae, *Halimeda*, mollusks, and benthic foraminifera being the most common skeletal constituents. Abundant nonskeletal grains, largely peloids, occur only in shallow lagoon areas of Glovers and Lighthouse Reefs. Carbonate mud on the southern Belize shelf (Matthews, 1966) and in the atoll lagoons (Gischler and Zingeler, 2002) is largely of biogenic origin. The curious occurrence of high-magnesium-calcite (HMC)-rich sediments on the northern Belize shelf is a consequence of either the disintegration of micritized HMC skeletal grains (Reid et al., 1992) or HMC precipitation (Macintyre and Aronson, 2006). Whittings, suspensions of fine-grained carbonate potentially indicating precipitation of  $\text{CaCO}_3$  in the water column, have been observed on the northern Belize shelf (Purdy and Gischler, 2003).

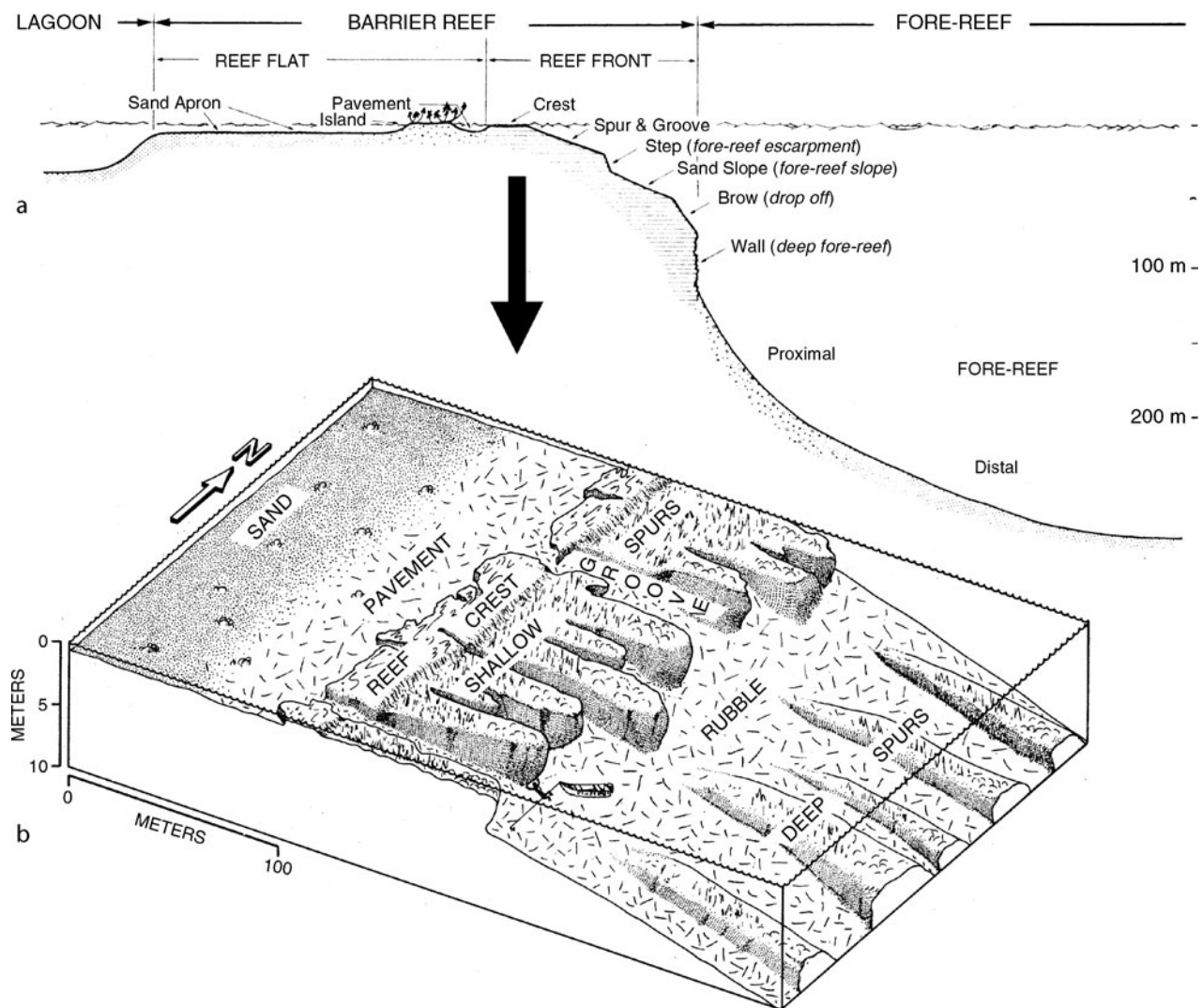


**Belize Barrier and Atoll Reefs, Figure 2** Three schematic cross-sections across Belize shelf and barrier reef from north to south.



**Belize Barrier and Atoll Reefs, Figure 3** Southern Belize shelf from the satellite (from Purdy et al., 2003).





**Belize Barrier and Atoll Reefs, Figure 4** Belize reef margins and zonations (after James et al., 1976; James and Ginsburg, 1979).

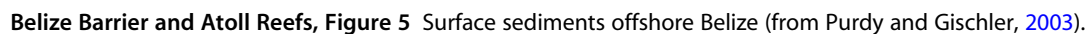
## Geology

The low northern part of Belize is largely covered by Cenozoic limestone. The mountainous south of the country (Maya Mountains) is characterized by Paleozoic siliciclastics and magmatic rocks, fringed by Cretaceous limestone and dolostone (Figure 6). A series of NNE-trending normal faults characterize the structural grain of the Belize passive continental margin. The hanging walls of these major faults form the basement of the Belize reef system. Offshore exploration wells and seismics have shown that up to 3.5 km of Meso-Cenozoic carbonates overlie the Paleozoic basement around the barrier reef (Purdy et al., 2003). Cenozoic carbonates on the offshore atolls are up to 1 km thick. The thickness of Pleistocene reefs ranges from 100 to 150 m. Studies on Pleistocene reefs are based on limited outcrops and a few deep wells in the northeastern and southern parts of the country

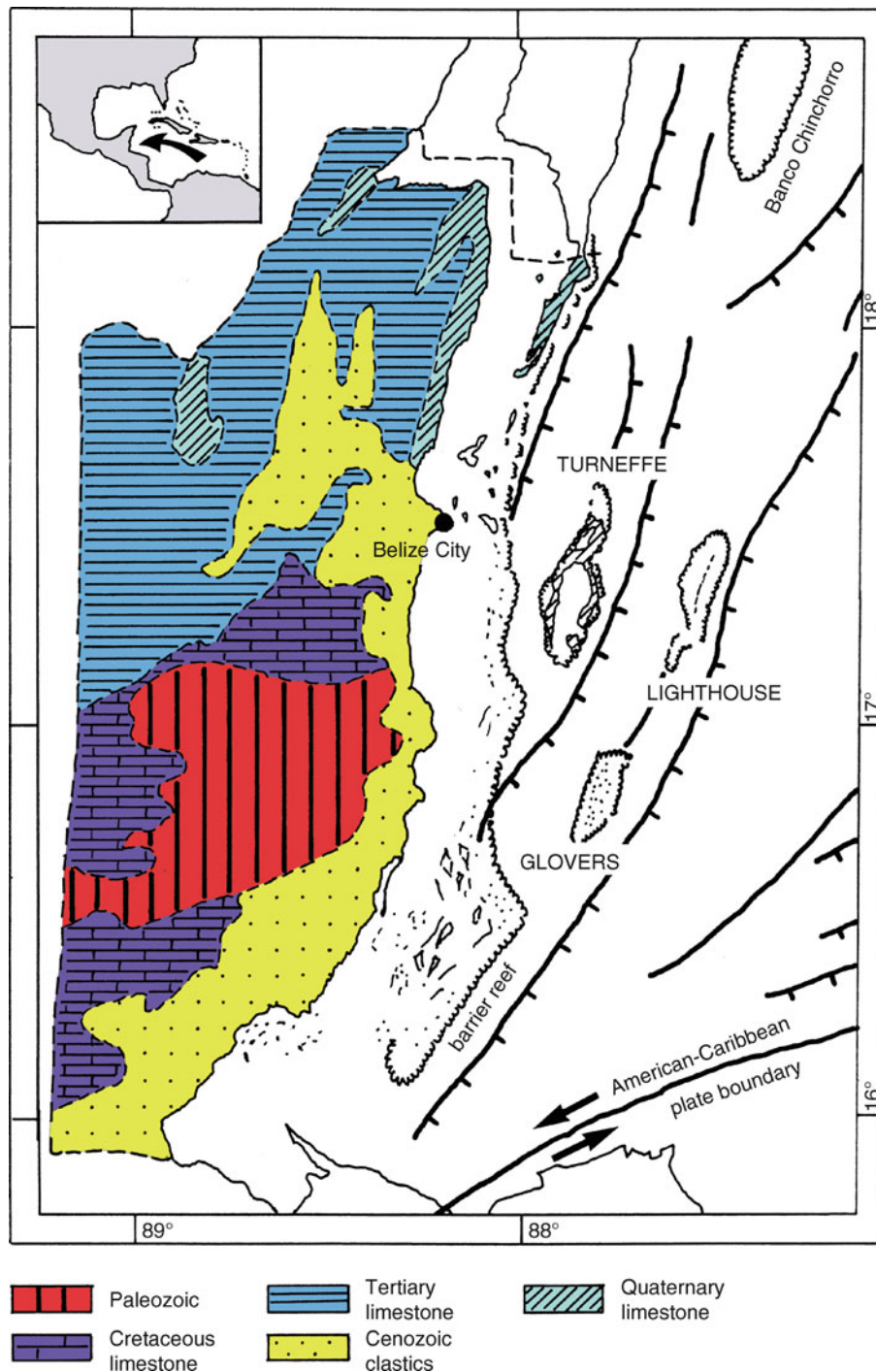
(Mazzullo, 2006; Gischler et al., 2010) as well as on Pleistocene reef limestone recovered in shallow coreholes below Holocene reef deposits (Gischler, 2006a). Pleistocene facies may be compared to modern ones, with the exception of the occurrence of Pleistocene oolites in northern Belize. Based on the sedimentologic and stratigraphic analysis of a long piston core taken in the deep forereef east of the barrier reef, Droxler et al. (2003) came to the conclusion that the modern barrier reef, as source of carbonate detritus, only came into existence during the exceptionally long and warm marine isotope stage 11, some 400 kyBP.

## Late Quaternary reef development, sea level, and antecedent topography

Postglacial reef growth started >8.26 kyBP on the Belize Barrier Reef (Gischler and Hudson, 2004) and 7.78 kyBP





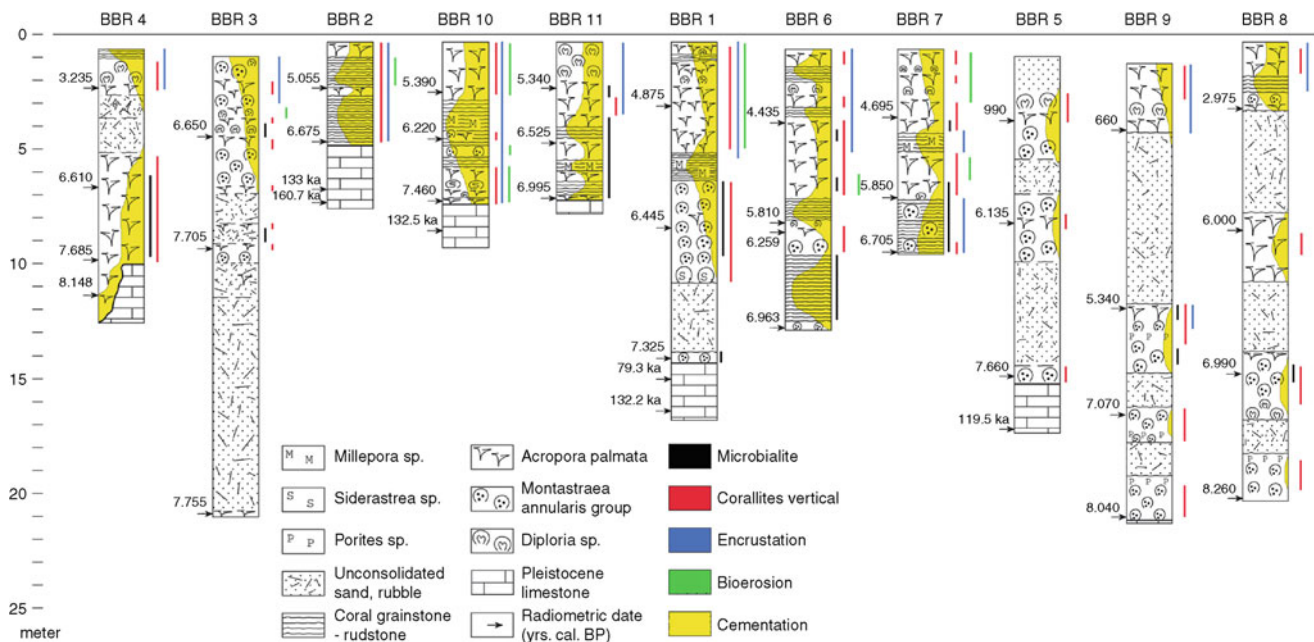


**Belize Barrier and Atoll Reefs, Figure 6** Simplified geologic-tectonic map of Belize.

on the offshore atolls (Gischler and Hudson, 1998) based on the analysis of shallow drilling (Figure 7). Holocene reef thickness ranges from 5 to >21 m (Gischler, 2008). Holocene reefs largely consist of branched (*A. palmata*, *A. cervicornis*) and massive (*Montastraea* sp., *Diploria* sp., *Siderastrea* sp.) corals, a well-cemented grainstone–

rudstone, and an unconsolidated rubble and sand facies. Reef accretion rates range from 0.46 to 7.5 m/kyr and average 3.03 m/kyr (Gischler, 2008). The Holocene sea-level curve of Belize is based on *A. palmata* and red mangrove radiometric age dates. The curve is transgressive and discussed controversially (Toscano and Macintyre,





**Belize Barrier and Atoll Reefs, Figure 7** Late Quaternary cores taken along Belize Barrier Reef, from north to south (from Gischler, 2008).

2003; Gischler, 2006b). Holocene reef lagoon development is ideally characterized by a succession of Pleistocene bedrock, dark soil, mangrove peat, shell bed (coquina), *Halimeda*-rich packstone, and mollusk-*Halimeda*-foram-rich wackestone and packstone, from bottom to top (Gischler, 2003). This succession is an expression of Holocene inundation by the rising sea and subsequent deepening. There is an ongoing controversy regarding the nature of the reef foundations. Based on coring, the basement of Holocene reefs on the offshore atolls and the barrier reef is Pleistocene limestone. Ferro et al. (1999) suggested that parts of the barrier reef platform were underlain by prograding siliciclastics, based on seismic investigations. The increase in reef thickness from north to south is thought to be an expression of both an increase in karst dissolution during Pleistocene sea-level lowstands and stronger subsidence in the same direction (Purdy, 1974; Gischler and Hudson, 2004). Holocene reefs on the Belize shelf are located both over Pleistocene limestone and siliciclastics (Purdy, 1974; Choi and Ginsburg, 1982). The former position of channel and river bars as well as incised valleys apparently was decisive for shaping antecedent topography and Holocene reef initiation (Esker et al., 1998; Ferro et al., 1999). Indeed, the rhomboid shape of some of the shelf reefs is reminiscent of channel bars. In addition, Lara (1993) and Purdy (1998) showed that faulting and folding was of importance for the formation of topographic highs and the subsequent initiation of reefs on the southern Belize shelf and southern barrier reef, respectively.

## Summary

The Belize reef system includes fringing, barrier, and atolls reefs as well as lagoonal patch reefs and lagoon atolls (faroos). The reefs, which are predominantly composed of corals (*Acropora* sp., *Montastraea* sp.) exhibit clear zonations. The Belize shelf is a classic example of a mixed carbonate-siliciclastic system, like many other large barrier reefs. Eleven modern sediment facies may be distinguished. The reef system of Belize is located on a passive continental margin with tilted fault blocks forming the basement. Both differential subsidence and variation in karst dissolution of underlying Pleistocene limestone determined patterns of late Quaternary reef accretion. Postglacial reef growth was extensive with thicknesses of >20 m and average accretion rates of 3 m/kyr.

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## Cross-references

[Antecedent Platforms](#)  
[Barrier Reef \(Ribbon Reef\)](#)  
[Eastern Caribbean Coral Reefs](#)  
[Great Barrier Reef Committee](#)  
[Holocene Reefs: Thickness and Characteristics](#)  
[Mangrove Islands](#)  
[Seagrasses](#)  
[Stoddart, David Ross \(1937–\)](#)  
[Western Atlantic/Caribbean, Coral Reefs](#)

## BERMUDA

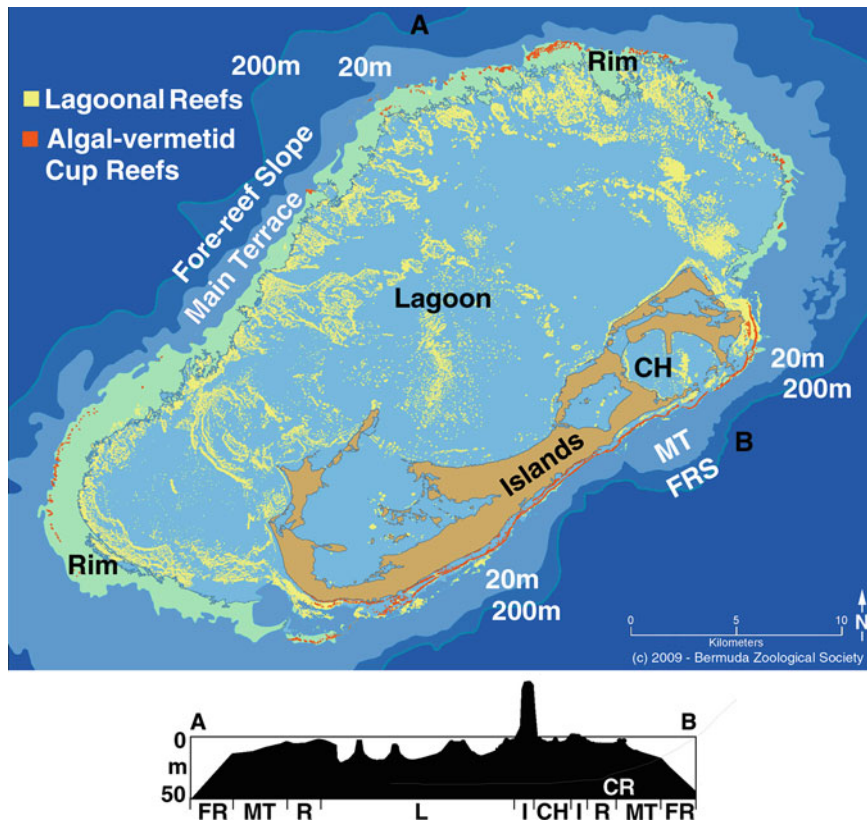
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## Definition and introduction

The British Overseas Territory of Bermuda, a crescent-shaped chain of about 150 islands, lies in the north-west Atlantic Ocean at 32°20'N and 64°45'W, about 1,500 km south of Halifax, NS. The regional setting and geological foundation of Bermuda's coral reefs are summarized in Logan (1992). Physiographically, Bermuda is an atoll, in that a peripheral annular reef tract and islands form a mostly submerged 26- by 52-km ellipse around



**Bermuda, Figure 1** Above: Aerial photograph of Bermuda, showing isobaths and main physiographic zones described in text. CH = Castle Harbour. A and B are end points of profile (below). Below: NW to SE profile across the Bermuda Platform along line A and B shown above: FR fore-reef slope; MT main terrace; R. rim; L. lagoon; I. Bermuda Islands; CH. Castle Harbour; CR. south shore algal cup reef tract (vertical exaggeration approx. 600).

a shallow central lagoon (Figure 1). The 20 m isobath separates this shallow platform from the fore-reef slope, with slopes of the latter rarely exceeding  $10^\circ$  seawards. The islands form the only emergent part of the Bermuda Seamount arising from 4,000 m depth and comprise a thin Pleistocene–Holocene carbonate sequence capping volcanic rocks below. The antecedent topography of this carbonate platform, formed from alternating periods of sediment movement and subaerial erosion in response to fluctuating Pleistocene sea levels, exerts a strong control over coral reef formation (Garrett and Scoffin, 1977), although the reefs are more than just veneers over the existing topography. Bermuda has the highest latitude reefs in the North Atlantic and owes its subtropical climate mainly to eddies of the warm Gulf Stream flowing into the Sargasso Sea. Nevertheless, the reefs show reduced biotic diversities compared to those in the Caribbean, with, for example, only about 40% of Jamaican coral and gorgonian species occurring in Bermuda but all of Bermudian species present in Jamaica (Logan, 1992; Logan, 1998). The coral *Acropora*, an important reef builder in the Caribbean, is a notable absentee in Bermuda, probably due to cool winter water temperatures, which average about  $18^\circ\text{C}$ .

### Major reef types and their communities

There are two major reef-building communities in Bermuda: a coral–algal consortium responsible for most of the reefs on and around the platform and the less common algal–vermetid gastropod cup reefs; found mainly around the edge of the platform, and particularly on the south-east side.

#### Fore-reef slope reefs

These reefs occur around the outside of the platform margin from 20 to 40 m depth and show total coral coverage values approximating 25%. The dominant corals, which account for over 85% of corals present (Logan, 1992), are large overlapping shingle-like colonies of *Montastrea franksi* (Figure 2) and domal heads of *Diploria strigosa* and *Montastrea cavernosa*. The bottom is highly irregular, with holes of 1–2 m relief between coral colonies. Understory species include *Porites astreoides* and *Diploria labyrinthiformis*, but coral diversity is low. Gorgonians are common, as is encrusting *Millepora alcicornis*, while coverage by species of the fleshy brown phaeophyte algae *Lobophora*, *Dictyota*, and *Stypopodium* can sometimes reach 25%, although this may be seasonal (Logan,





**Bermuda, Figure 2** Large colony of *Montastrea franksi* showing overlapping shingle-like growths, fore-reef slope reefs, North of North Rock, 28 m.



**Bermuda, Figure 3** Head corals and gorgonaceans in shallow wave-surge area, movement left and right. Note alignment of sea fans normal to wave direction, rim reefs of North Rock, depth 4 m.

1998). Because of their depth and distance from land, these reefs are the poorest known in Bermuda.

#### Main terrace reefs

These reefs succeed the fore-reef slope reefs at the platform margin, covering a prominent terrace extending from 10 to 20 m seawards from the annular rim reefs. From a narrow sediment apron at the outer edge of the rim reef tract, at a depth of about 5 m, a series of reef ridges, separated by sand channels, form an anastomosing pattern similar to spur-and-groove structure. This feature is particularly well shown along the western edge of the platform (Logan, 1988). Total coral coverage values for main terrace reefs are the highest in Bermuda, frequently reaching 50%, but coral diversity is again low. The bottom has less relief than that of the fore-reef slope and is dominated by domal colonies of the two species of *Diploria* (64%), encrusting or platy *Montastrea franksi* (32%), and domal *Porites astreoides* (3%). This *Diploria*–*Montastrea*–*Porites* reef-building community is typical of all platform margin and lagoonal coral–algal reefs across the platform.

#### Rim reefs

Rim reefs are developed on the elevated 100-km ring of shallow shoals that encircle the lagoon and protect it from open-ocean waves. These reefs extend lagoonwards by lobate extensions and grade into main terrace reefs on the seaward side. Their tops lie between 2 and 6 m depth and are dissected by ramifying sand channels of about 10–15 m depth. The reef tops show relief of about 1 m between coral heads, with about 22% coral coverage (Dodge et al., 1982). Large gorgonaceans belonging to at least six genera are attached to the reef tops and channel sides, taking advantage of the almost constant surge from the open ocean (Figure 3). The *Diploria*–*Montastrea*–*Porites* coral assemblage is again predominant, their



**Bermuda, Figure 4** Cavity at the base of reef between sand channels, rim reefs, North Rock, 9 m depth.

species accounting for over 90% of the coral coverage, with the two species of *Diploria* accounting for over 65% alone. A wide variety of coral growth forms occurs, from domal to encrusting to platy, presumably in response to varying light conditions. Sponges, zoanthids, hydrozoans, anemones, and corallimorphs are common, with smaller colonies of less common coral species present as understory species. Diverse coelobite communities colonize shaded areas beneath coral heads or in caves and tunnels near the base of the reef (Figure 4). While occasional diseased coral colonies are encountered, the rim reefs remain the most healthy and attractive reefs in Bermuda and appear to have been little affected by bleaching or anthropogenic influences.

#### Algal–vermetid cup reefs

These cup reefs, locally known as “boilers,” occur as a discontinuous tract on the outer edge of the platform

rim, particularly on the south-eastern side from St. David's Head to South-West Breakers, where there are three distinct zones, more or less parallel to the shoreline. The first zone comprises bioconstructional lips attached to headlands, the second is the present actively growing cup reef tract at the edge of the narrow rim (near-shore platform), and the third and oldest zone consists of drowned cup reefs furthest from the shore whose tops now lie at a depth of 10–12 m (Meischner and Meischner, 1977). These authors suggest that the latter were formerly at sea level about 7,000 years ago and that the bioconstructional lips will eventually become the actively growing tract as headlands are eroded. Cup reefs are generally circular to oval in shape (Figure 5) and less than 30 m in their maximum dimension. In profile they have an elevated rim awash at high tide, enclosing a shallow mini-lagoon with occasional small coral heads, and tapering to a narrow undercut base at 8–10 m depth (Logan, 1992). Void space is high in these reefs. The main constructive agents are crustose coralline algae and the partially embedded vermetid gastropod *Dendropoma corrodens*, with occasional encrusting *Millepora alcicornis*, all of which are adapted to turbulent conditions in high wave energy environments (Thomas and Stevens, 1991). Boring by sea urchins and sponges and intense

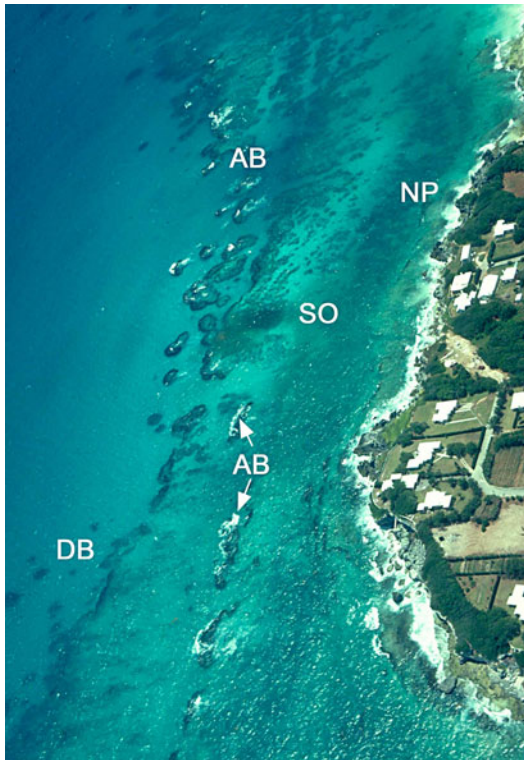
grazing by parrotfish are the main destructive agents. The algal-vermetid cup reefs represent an unusual reef type rarely found elsewhere in the world.

### Lagoonal reefs

Lagoonal reefs comprise patch reefs of many sizes and shapes in North Lagoon (Logan, 1992), the tops of which are close to the surface, with steep flanks grading off into lagoonal sands and muds at depths averaging 15 m. Coral coverage on the tops of lagoonal patch reefs is generally less than 40% (Dodge et al., 1982; Murdoch, 2007), although the flanks often reach 70% with species of *Diploria* and *Porites* dominating the outer reefs, *Montastrea* the central areas, and *Madracis* the nearshore reefs (Murdoch, 2007). The lagoonal reefs have higher coral diversity than the platform reefs, and in addition, support a rich sessile invertebrate biota of corals, gorgonaceans, zoanthids, sponges, anemones, tunicates, and bivalves, as well as a variety of calcified algae which act as sediment producers and binders. Grazing parrotfish increase in diversity and abundance as distance from land increases and are prodigious producers of fine sediments. The hydrozoan *Millepora alcicornis* in branching and encrusting growth forms is present on all lagoonal reefs, the branching form being particularly common on the nearshore reefs along the north shore.

### Inshore reefs

Of Bermuda's inshore waters, only Castle Harbour has significant reef development, where linear fringing reefs occur around the western and southern shorelines, and steep-sided patch (pinnacle) reefs are present in the north-western and south-eastern areas. Dredging for airport construction in 1941–1943 resulted in hydrographic changes and resuspension of fine sediments in the area which has had deleterious effects on both of these reef types (Dryer and Logan, 1978; Logan, 1992). Prior to the dredging, the waters of Castle Harbour were pristine and supported healthy reefs (see predredging accounts in Dryer and Logan, 1978); now living corals show only about 5% coverage on fringing reefs and 13% on patch reefs. The patch reefs are mainly of the pinnacle type, about 4–5 m high and 5 m wide, with irregular tops at depths of 1–2 m and with vertical or steep-sided walls. Dryer and Logan (1978) reported *Isophyllia sinuosa* and *Diploria labyrinthiformis* as the dominant corals on the reef tops, with coral coverage and diversity low, while the steep flanks showed relatively high coral coverage values of up to 50% by branching corals of *Oculina* and *Madracis* which are able to shed fine sediments efficiently. Since then, resurveys of Castle Harbour reefs by Cook et al. (1994) and Flood et al. (2005) indicate that *Diploria labyrinthiformis*, an efficient sediment shedder, is still the dominant species on reef tops, but active recruitment of *D. strigosa* is increasing the importance of this species. The branching coral *Madracis auretenra* continues to rank high in coverage on the pinnacle reef flanks,



**Bermuda, Figure 5** Aerial photo off Hungry Bay, south shore of Bermuda, showing nearshore platform (NP), line of actively forming cup reefs (boilers AB), drowned older boilers (DB), and dark smudge of sewage outfall (SO).



but *Oculina diffusa* appears to have declined since the 1978 survey, although Flood et al. (2005) suggest that this may be an artifact of the different survey methodologies used.

### Factors affecting Bermuda's reefs

While factors such as coral competitive interactions, reproductive activity, growth rates, and diseases can affect the composition of Bermuda's reefs (Logan, 1992, 1998), coral bleaching, pollution, and ship groundings are presently regarded as the most important, since they may pose a threat to the health of Bermuda's reefs in the long term.

### Coral bleaching

Episodes of extensive bleaching in Bermudian corals, coincident with periods of elevated summer water temperatures, occurred in 1988, 1991, 1997–1998, and 2003, with minor bleaching in other years, but the long-term impact of these episodes has been remarkably slight, with coral mortality low at less than 2%. The most detailed studies were done on the 1988 and 1991 events by Cook et al. (1990, 1994) who showed that in both years the species most affected was the hydrozoan *Millepora alcicornis*, with lesser effects on *Montastrea franksi*, *Diploria labyrinthiformis*, and *Porites astreoides*. In 1988 water temperatures were the highest in the previous 38 years (over 28°C offshore), with platform margin rim reefs the most affected. In contrast, Bermuda's lagoonal reefs experienced the most bleaching in the 1997–1998 bleaching event, with *Millepora alcicornis* again the most affected species. Cook et al. (1990) suggested that Bermuda's high latitude corals are thermally sensitive to elevated temperatures that are within the normal thermal tolerance range for corals at lower latitudes, indicating that thermal tolerance in reef corals is inversely related to latitude.

### Pollution and ship groundings

Jones (2008) surveyed main terrace coral reefs lying 300 m from a daily discharge of 2.5 million liters of untreated sewage from the Hungry Bay outfall on the south shore of Bermuda. He concluded that there is little or no evidence of adverse environmental effects on the reefs over the previous decade, in terms of species composition, abundance, and incidence of coral diseases.

The resuspension of sediments by dredging in Castle Harbour has already been mentioned, but sediment resuspension by ship propellers is another form of anthropogenic pollution which can have harmful effects on reefs. Unfortunately, most of this takes place through two shipping channels that cross the central lagoon where otherwise healthy reefs are abundant. Increases in the sizes of ships have led to a call to dredge and substantially alter the path of the shipping channels, which is likely to have a harmful effect on the condition of lagoonal and rim reefs.

A previously serious problem was the effect of ship groundings, which was studied by Cook et al. (1994). They listed the major ship groundings from 1940 to

1993 and concluded that damaged sites have been extremely slow to recover, mainly because of poor recruitment and slow growth of corals, particularly *Diploria* (Smith, 1992). They estimated a period of 100–150 years for coral coverage and species diversity to be restored on such reefs. Predictably, reef fish populations in these areas have been reduced and may remain so until sufficient coral growth has accrued. One further problem is the possible inhibition of recruitment from biocides in antifouling paint from the hulls of grounded ships (Jones, 2007). To prevent any further risks to the Bermuda reefs, the Bermuda government has set up a sophisticated radar surveillance system which has effectively prevented further grounding since 1993. This system permits the monitoring of vessel movements to ensure that they keep clear of the International Maritime Organisation (IMO) and International Association of Marine Aids to Navigation and Lighthouse Authorities (IALA)-sanctioned Area To Be Avoided – a 20 nautical mile “no go” zone around the island to protect Bermuda's reefs. However, since 2000, a dramatic increase in marina and nearshore development, the addition of larger cruise ships, and a new ship pier appear to be just the start of an increase in large-scale negative impacts on the marine environment, indicating the need for stronger planning policies and better resource management.

### Summary

Bermuda at 32°N supports the highest latitude coral reefs in the North Atlantic and one of the highest in the world. Algal-vermetid cup reefs, particularly well developed off the south shore of the island, represent an unusual reef type rarely found elsewhere in the world. While corals, the main reef builders, show lower diversity than the Caribbean, presumably in response to cool winter water temperatures, nevertheless the main physiographic zones of fore-reef slope, main terrace, rim, and lagoon all support thriving coral reefs which have as yet been little affected by coral bleaching or anthropogenic influences such as pollution and ship groundings. Only reefs in the inshore waters of Castle Harbour have suffered long-term deleterious effects from extensive dredging for airfield construction in 1941–1943. However, there is a need for stronger planning policies and better resource management in the whole area if the Bermuda reefs are to remain healthy and protected.

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### Online sites (URLs)

- Bermuda Reef Ecosystem Assessment and Mapping Programme (BREAM): <http://www.bermudabream.org>
- Bermuda Zoological Society's aerial mosaic of Bermuda's reef platform, hosted by LookBermuda: <http://www.lookbermuda.com/PhotoMap/800x600.html>
- Marine Environmental Program (MEP) at Bermuda Institute of Ocean Sciences (BIOS): <http://www.bios-mep.info>

### Cross-references

Acropora  
Antecedent Platforms  
Atolls  
Forereef/Reef Front  
Geomorphic Zonation  
Patch Reefs: Lidar Morphometric Analysis

## BIKINI ATOLL, MARSHALL ISLANDS

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### Definition

Bikini Atoll lies in the northern Marshall Islands in the central Pacific. It is 694 km<sup>2</sup> with a perimeter of 122 km. Its central lagoon is up to >30 m deep. There were originally 25 islands on the rim but several of these were destroyed by the Nuclear testing carried out on the Atoll in the 1950s.

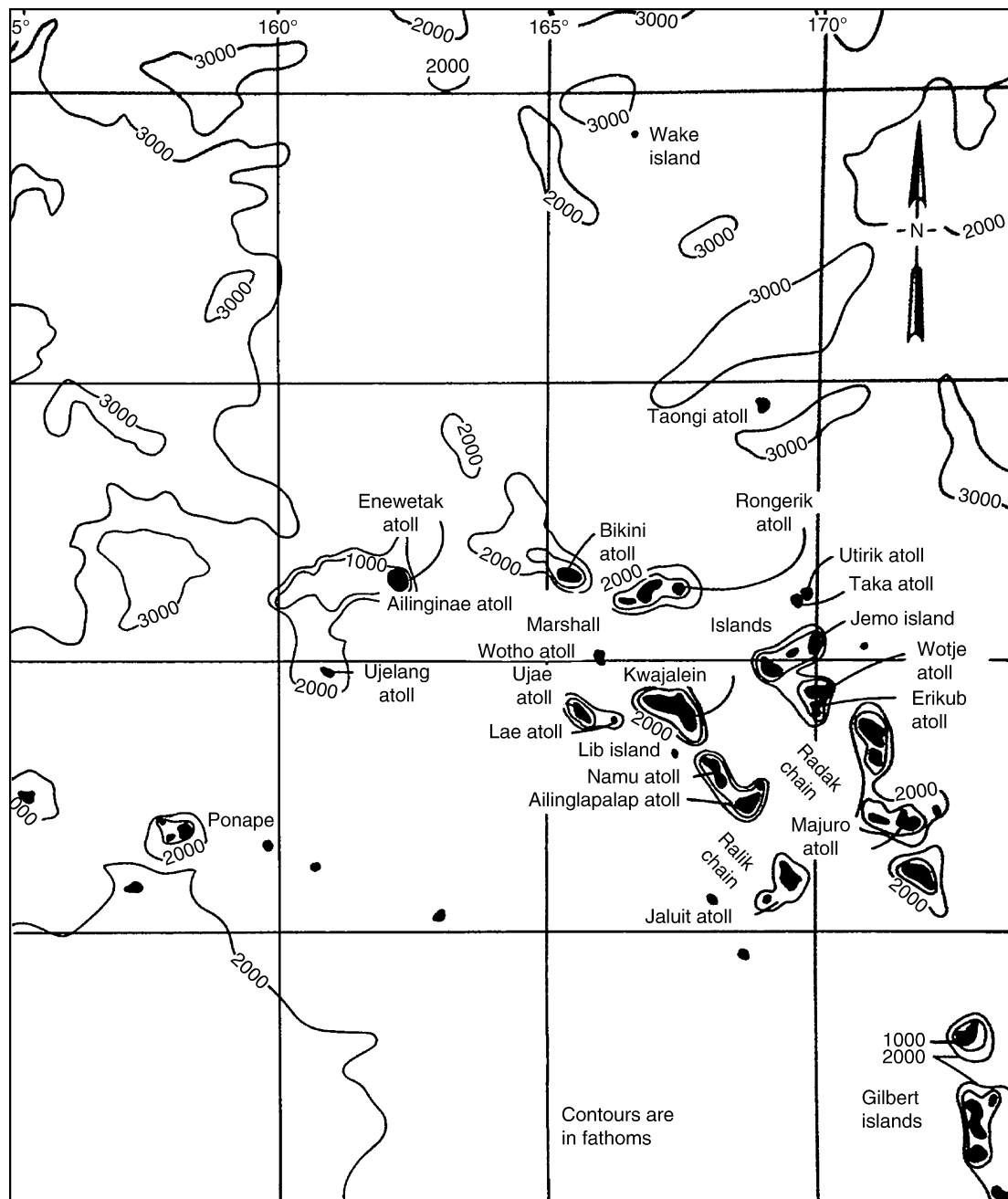
### Introduction

The Marshall Islands archipelago consists of 29 atolls and five isolated reef islands with a combined total of 1,136 low reef islets, 174 km<sup>2</sup> of land areas, 13,000 km<sup>2</sup> of lagoon areas, and 2,600 km of reef circumferences. As a whole, the Marshall Islands are located in Micronesia, situated at the east of the Mariana Islands, northeast of the Caroline Islands, and northwest of the Gilbert Islands (Figure 1). The Marshall Is. support the oldest and largest atolls in the Pacific and the world and consist of two northwest to southeast trending ridges, the *Ralik* to the west and *Ratak* to the east, each with separate atolls, islands, cultural lineages, and traditional leadership. Bikini Atoll (11° 37' N and 165° 23' E) is at the north end of the western chain, with its closest neighbors Enewetak and Ujelang atolls lying 150–200 km to the west, and Rongelap and Ailinginae Atolls 50 km to the east.

Bikini is a rectangular atoll, with its long axis being 46 km from east to west, and varying from 15 to 19 km along the north–south axis (Figure 2). The combined reef and lagoon area of the atoll is 694 km<sup>2</sup>, total land area is about 6 km<sup>2</sup>, and total perimeter reef circumference is 122 km. Bikini consisted of 25 islands until two and a half of them were destroyed by the hydrogen bomb “Bravo” test in 1954. Overall, Bikini Atoll ranks tenth in terms of total reef and lagoon area and 11th in terms of land area among the Marshall Islands. Bikini lies in the northern arid Marshall Islands and supports less vegetation, groundwater, rainfall (1450 mm per year), and human populations compared to those in the central and southern Marshall Islands. However, rainfall is highly variable ranging from 600 to 2,400 mm per year. Surface ocean water temperatures normally range from 25 to 29°C per year.

### Physical environment

Bikini's low coral islets are 3–4 m above the mean sea level and concentrated on the east and southwest rims of the atoll. The western and northeast rims emerge at low tide but are nearly devoid of islets. The largest islet, Bikini (2.14 km<sup>2</sup>) is at the northeast corner of the atoll, and the four next largest islets in descending size are Eneu (Enyu)



**Bikini Atoll, Marshall Islands, Figure 1** Vicinity map of eastern Micronesia and the Marshall Islands (after the Bikini Atoll Rehabilitation Committee, 1987).

at the southeast corner, Nam on the northwest rim, Enidrik on the southeast rim, and Aerokojlol on the south rim. All eight of the passes at Bikini cut through the elongated south rim of the atoll, with the longest (16 km) and shallowest (5–20 m depth) pass at the southeast corner of the atoll just west of Eneu Island. A cluster of seven narrow but deep passes (>30 m) bisect the southwest perimeter reef. The prevailing northeast trade winds generate

wind waves that break on windward reefs and, via wave set-up, continually drives water across the reef flats into the northeastern lagoon regardless of the state of the tide. These cooler waters then sink toward the bottom of the lagoon, spiral within broad cells, and eventually discharge through the passes and over leeward western reef crests (Figure 3). The eastern lagoon is calm and sheltered from the trade winds by the eastern perimeter reef and islands.



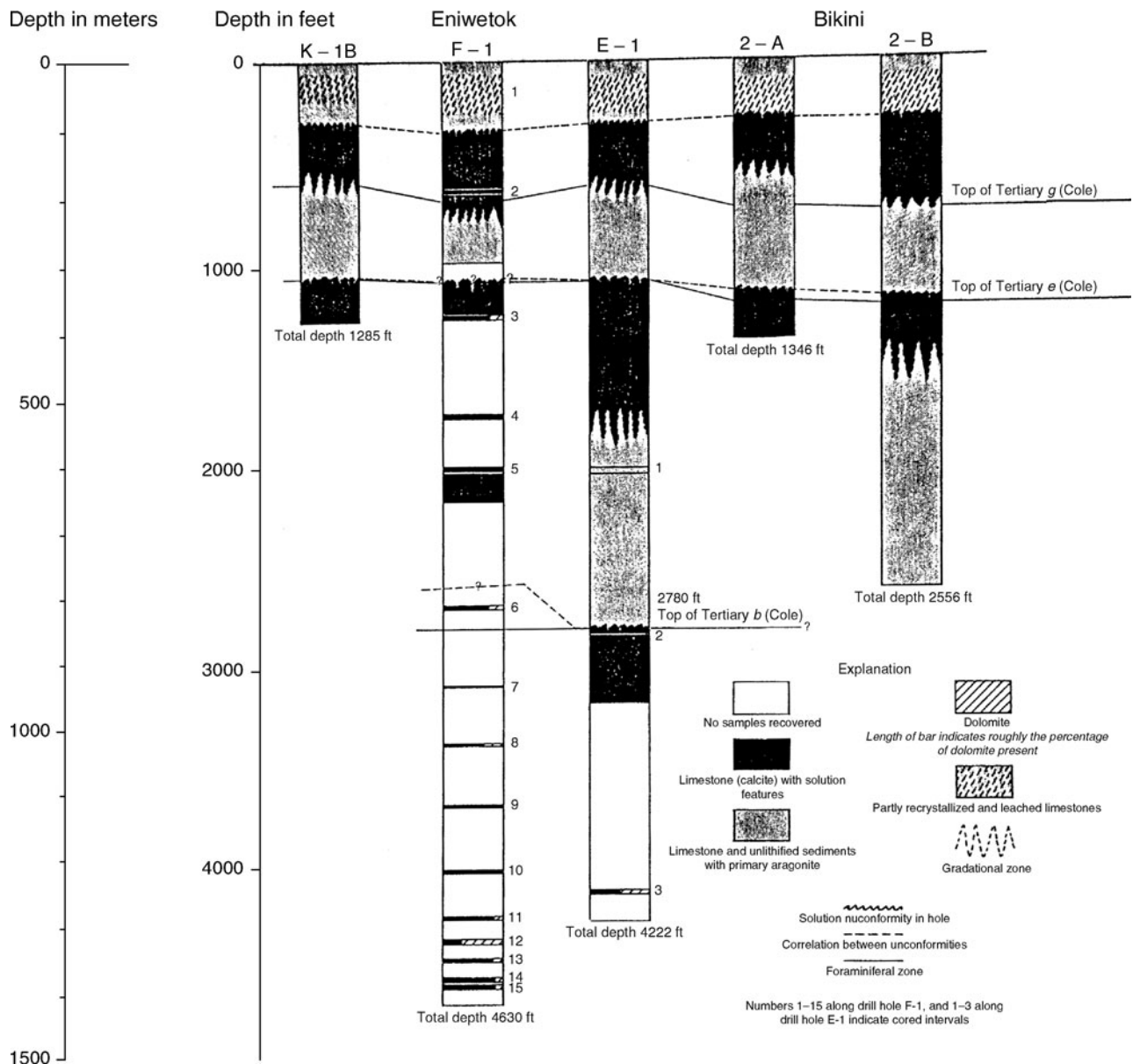


However, the wind fetch 20 km or more to the west generates steep wind waves of up to 2 m in height in the central and west lagoon during normal wind conditions, rendering small boat navigation hazardous during the heavy winds and seas.

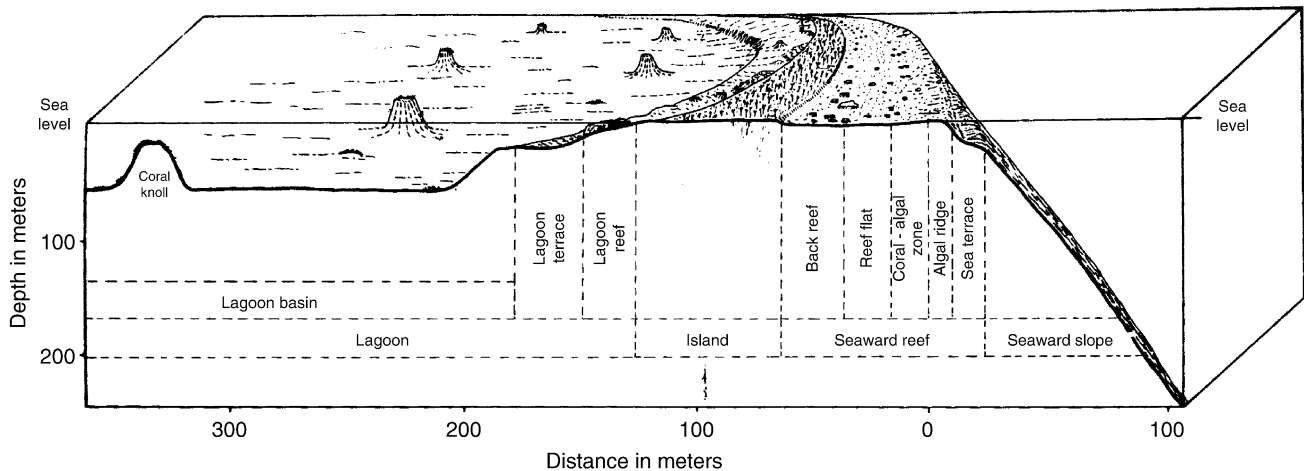
### Scientific surveys at Bikini Atoll

The geological structure, composition, and morphology of Bikini Atoll were thoroughly studied before and after the initial Operation Crossroads atomic bomb tests at Bikini in 1946. Samples were collected at many sites via shallow hookah diving, free-diving, and by hand on shallow patch reefs in the lagoon and on both sides of the perimeter reef

and reef crests in 1946–1947. Extensive collections were also made of corals and geological samples via dozens of deep dredge hauls of the lagoon floor and seaward fore reefs to depths of 60 m and more. Two deep drill cores were also obtained and analyzed from Bikini and later compared to those taken at Enewetak (Figure 4; see also *Enewetak Atoll, Marshall Islands*). The two Bikini drill holes penetrated to depths of 1,346 and 2,556 ft and extended well into Tertiary reef deposits but did not reach basalt volcanic rock as was the case for the Enewetak drill holes. The bottom half of the longer of the two Bikini cores was mostly composed of unlithified sediments and primary aragonite, yielding fossil corals, calcareous algae,



Bikini Atoll, Marshall Islands, Figure 4 Comparative composition of Bikini and Enewetak drill cores (after Schlanger, 1963).



**Bikini Atoll, Marshall Islands, Figure 5** Vertical cross section and geomorphological zones along the windward reef rim of Bikini Atoll (after Emery et al., 1954; Ristvet, 1987).

and foraminifera. The intervals and Pleistocene unconformities in the Bikini cores were consistent with those of the Enewetak cores. After a hiatus of 2 decades, more recent studies on archaeology, corals, vegetation, birds, sea turtles, and fish were accomplished in the mid 1980s, with corals and fish surveyed again in 2002.

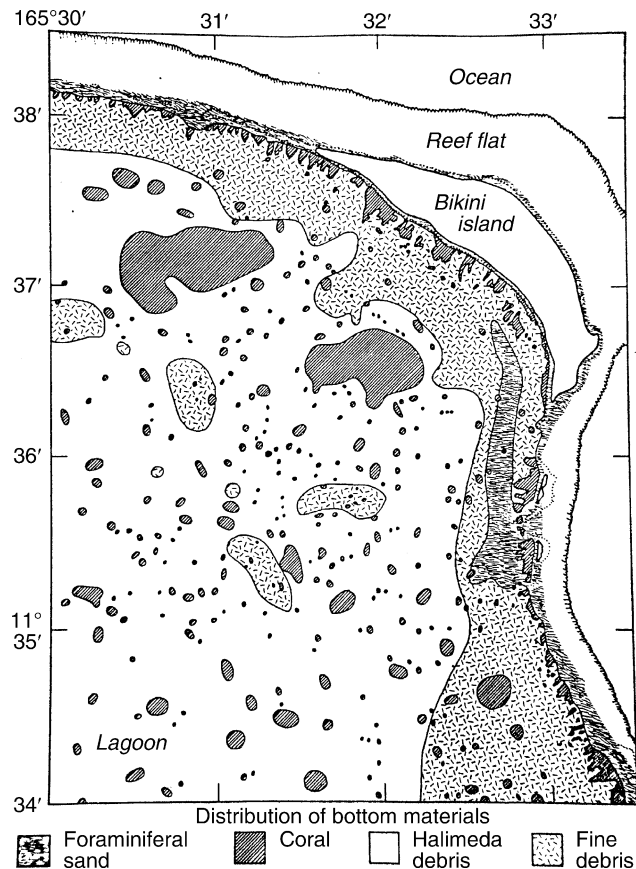
The geomorphology of windward reefs and the east lagoon was extensively mapped and studied. Reef characteristics at Bikini were found to be similar to those of Enewetak and other atolls in the Marshall Islands. Major reef zones along the windward side of the atoll from off-shore to the lagoon are diagrammed on Figures 5 and include:

- Seaward slope
- Sea terrace
- Algal ridge
- Coral algal zone
- Seaward reef flat
- Islet or inter-island reef crest
- Lagoon reef flat
- Lagoon terrace
- Lagoon floor or basin
- Coral knolls (pinnacle and patch reefs)

Exceptional galleries (room and pillars) have also been reported on the windward reef flat off Bikini Island. Numerous patch and pinnacle reefs were surveyed and studied at Bikini throughout the lagoon, and eastern lagoon sediments were mapped in detail (Figure 6).

### Marine biology

Extensive surveys of stony corals were accomplished at Bikini by three separate investigators in 1947–1948, 1985, and 2002. When combining the updated and corrected lists of all three, 283 species of shallow stony corals have been reported from Bikini, the most of any surveyed atoll in the world. In addition, John Wells



**Bikini Atoll, Marshall Islands, Figure 6** Composition of lagoon sediments in the eastern rim of Bikini Atoll (after Emery et al., 1954).

also reported fossil species and a dozen deep water azooxanthellate stony corals species (Wells, 1954a, b). The high numbers of contemporary species are attributed to the extensive combined observation and collecting

efforts in all major habitats, deep and shallow at Bikini. In comparison, lesser collecting and observational efforts to depths of 30 m have yielded about 180 species of stony corals at Enewetak, 175 at Arno, 180 at Ailinginae, 205 at Majuro (the second highest totals to date in the Marshall Islands), and 203 species at Helen Atoll in southwestern Palau. The latter Bikini surveys in 1985 and 2002 relied primarily on scuba diving, and both documented prolific recovery of corals within 27–44 years of the end of the nuclear testing program.

The first comprehensive fish surveys in 1985 were focused on estimates of species likely to be consumed by the returning Bikini People and are not a comprehensive inventory of all species. Yet, 250 species at 29 sites were reported by Agegian et al. (1987). Later, Pinca et al. (2002) independently conducted fish surveys at Bikini and accounted for 359 species, but a combined list of both the investigations was not compiled. Randall and Randall reported more than 800 fish species at Enewetak based on extensive observations and diverse collections including poison stations to account for cryptic species. Thus, the higher diversity of fish species at Enewetak is attributed to considerably more survey effort and methods. In comparison, 267 fish species were reported at nearby Ailinginae Atoll at 33 sites in 2002. As with the 1985 Bikini survey, the emphasis on the Ailinginae surveys included preferential attention to larger fish, and thus, many cryptic and smaller species were not inventoried. Bikini fish biomass and abundance was reported high in both fish surveys.

## Vegetation

Fosberg (1988) surveyed ten islets including four of the five largest at the atoll in 1985, (Figure 7). He organized his surveys based on prior analysis of aerial photographs of Bikini obtained during the 1978 radiological aerial survey of the Northern Marshall Islands (see Tipton and Meibaum, 1981). Fosberg compiled 65 plant species and noted that most native species were still present at the atoll including stands of the beach forest tree *Pisonia*, a globally imperiled IUCN red-listed genus, on several islets on the western half of the atoll. However, other intact stands of native vegetation were decimated from copra production during the German and Japanese occupations and followed by nuclear weapons testing and related infrastructure development. Fosberg's overall conclusion was "On the islets mapped in any detail for the present survey, no unaltered vegetation has survived. . . The present vegetation still contains most of the species present in pre-nuclear times. . . and a few species have disappeared. In addition a number of exotics have appeared and some have become common. . . Recovery of vegetation after the nuclear tests has been rapid, but with a high proportion of pioneer species." Fosberg recommended protective status for the six tiny islets on the southwest reef on the basis of their high natural diversity and bird and turtle populations.



**Bikini Atoll, Marshall Islands, Figure 7** F. Raymond Fosberg surveying the vegetation at Bikini Atoll in 1984 (source: J.E. Maragos).

## Seabirds and shorebirds

Bird surveys were conducted by Garrett and Schreiber at 12 islets at Bikini Atoll in May 1986, and they compiled a combined total of 26 bird species compared to an earlier survey of 17 birds in 1969, three of which were not seen in the 1986 survey. The higher latter totals were attributed to much greater survey effort and revealed the presence of 14 species of seabirds and a resident reef heron, with ten of the seabird and the heron species likely nesting at Bikini. The seabirds included four shearwaters: (*Puffinus pacificus*, *P. bulleri*, *P. griseus*, *P. tenuirostris*), Red-tailed Tropicbird (*Phaethon rubricauda*), Great Frigatebird (*Fregata minor*), Red Footed and Brown boobies (*Sula sula*, *S. leucogaster*), four terns (*Sterna bergii*, *S. sumatrana*, *S. oahuensis*, *Gygis alba*), two Noddies (*Anous stolidus*, *A. minutus*), and the Eastern Reef Heron (*Egretta sacra*). Additionally, migratory species included the Laughing Gull (*Larus atricilla*) and seven Arctic shorebird species: Lesser Golden Plover (*Pluvialis dominica*), Wandering Tattler (*Heteroscelus incanus*), Gray-tailed Tattler (*H. brevipes*), Whimbrel (*Numenius phaeopus*), Bristle-thighed Curlew (*N. tahitiensis*), Ruddy Turnstone (*Arenaria interpres*), and Sanderling (*Calidris alba*). Three of the bird species: Buller's Shearwater (*P. bulleri*), Sooty Shearwater (*P. griseus*), and the Curlew are red-listed by IUCN.

At-sea observations by the ornithological team revealed 12 species including one species, the Pomarine Jaeger, not reported during land surveys at Bikini Atoll. Overall,



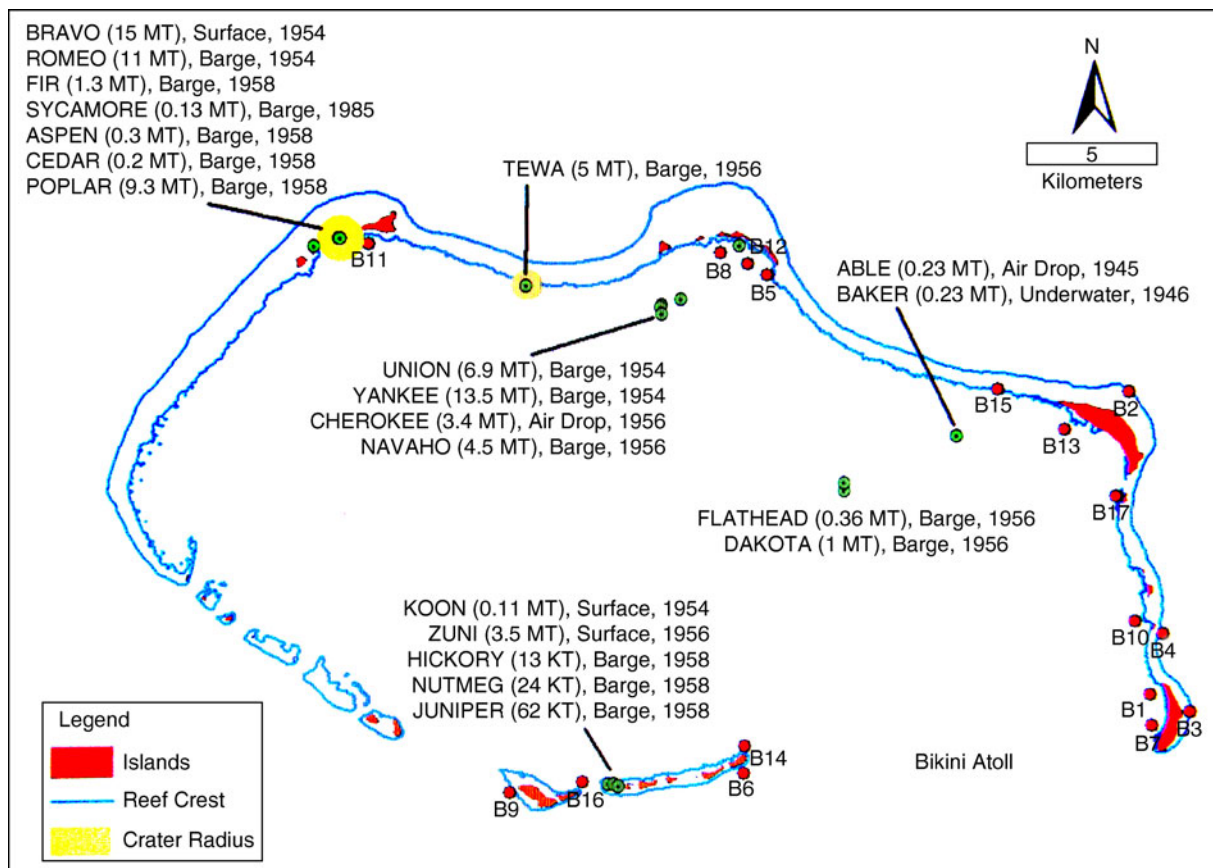
the 1986 team concluded that the avifauna of Bikini is “typical of low coral atolls in the region, with significant nesting populations of several species of seabirds. . . It is likely that most or all current populations of Bikini Atoll seabirds represent recolonization occurring after the conclusion of atomic bomb testing.” The presence of many ground-nesting seabirds at the atoll suggests that some of the outer islets were free of rodents, although the latter were noticeably abundant on the main islands. Birds were again surveyed at Bikini in 2002, and the authors suggested that the absence of islanders at the atoll over many years may be benefiting seabird populations.

### Sea turtles

Hawksbill turtles (*Eretmochelys imbricata*) and green turtles (*Chelonia mydas*) were commonly observed swimming on ocean reefs and lagoon habitats during marine biological surveys from 1984 to 1986. The seabird team, Garrett and Schreiber (1988) also searched for turtle tracks and pits during their surveys of 12 islets in 1986, and they reported seeing a few nests and tracks only at Bikini Island.

### Atmospheric nuclear tests at Bikini

The nuclear program at Bikini totaled 23 tests from 1946 to 1958 and was the first site for the U.S. Pacific Proving Ground. The location, yield, crater diameter (if any), and code name for each test are provided in Figure 8. The first two tests, *Able* and *Baker* of Operation Crossroads in 1946, were conducted 5 km east of the north end of Bikini Island. At the time, WWII had just ended, and there was little knowledge of the destructive power of fission bombs. The goal of Operation Crossroads was to determine whether such weapons could disable and sink large warships in battle-ready condition (fully armed and fueled). The two detonations were public events, witnessed by politicians and press from many nations. Hundreds of American warships with approximately 42,000 sailors participated in the tests, with the manned ships anchored at increasing distances away to observe and document the effects of the blasts. About two dozen unmanned and derelict vessels, including three captured during the war, were placed as targets near ground zero, and about half of the occupied ships were positioned close enough to be intentionally exposed to radioactive fallout from the blasts to assess its effects. Several ships carried livestock as



**Bikini Atoll, Marshall Islands, Figure 8** Map showing location, crater size, code name, yield, and date of 23 nuclear tests at Bikini Atoll from 1946 to 1958 (after Richards et al. 2008).

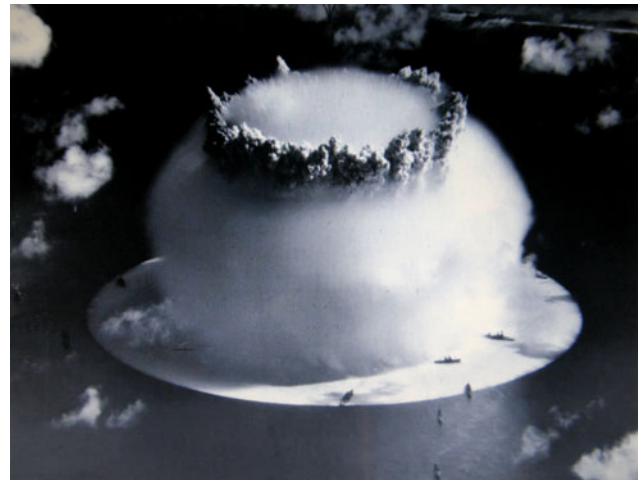


**Bikini Atoll, Marshall Islands, Figure 9** Baker atomic bomb test in east Bikini Lagoon, 1946, showing upward entrainment of two target ships in the cylindrical upheaval of seawater just after detonation (source: U.S. Government photo).

a proxy for assessing the possible impact of radiation on humans.

The first test *Able* was an air drop that detonated at 300 m above the lagoon within 1 km north of the targets, and results of the test were inconclusive although several of the ships were sunk. The device for the second test *Baker* was submerged at a depth of 30 m in the lagoon, and its detonation instantaneously thrust over 1,500,000 m<sup>3</sup> of contaminated seawater a mile high within the first second (Figure 9) carrying at least two ships with it. In turn, this generated huge waves radiating away from the blast that tossed large warships out of the water and sinking eight of them. Although never noted, these waves may have washed up on nearby Bikini Island, possibly responsible for contaminating the potable groundwater beneath the island that later proved to be a major hurdle for the resettlement of the island. The *Baker* test also evaporated vast amounts of seawater, creating a massive radioactive condensation cloud that contaminated many of the islands and manned ships (Figure 10). After the second test, the crews for the flotilla of observer warships swabbed, scrubbed, and washed down their decks but could not rid radioactivity from many of the vessels. The ships and crews then returned to ports scattered all over the globe. Some of the contaminated ships were too “hot” and were sunk. Less information is available on the fate of their crews. Baker appears to have been the first and last open underwater test during Marshall Islands nuclear era.

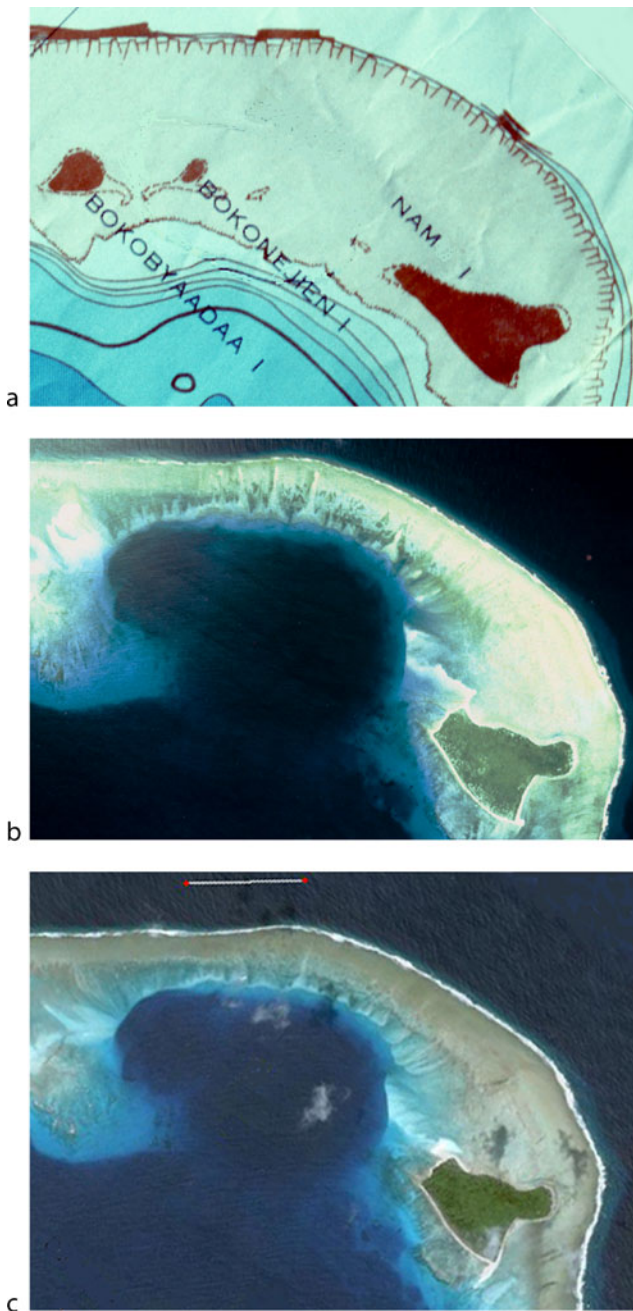
After a hiatus of 8 years, additional nuclear tests at Bikini were conducted from 1954 to 1958 (Figure 8). These were much further to the west of the main inhabited islands, and all were surface or barge detonations except one additional airdrop (Dakota 1956, 1 megaton (MT) yield). During the Operation Castle, six very large tests from 6.9 to 15 MT were detonated along the north rim near Aomen and Nam Islands and included one fizzle (Koon) along the south rim near Enemaan Island. The largest



**Bikini Atoll, Marshall Islands, Figure 10** Baker atomic bomb test in east Bikini Lagoon, 1946, showing expansion of condensation cloud shortly after detonation (source: U.S. Government photo).

atmospheric test in history was the Bravo blast detonated at the end of a reef flat causeway 970 m southwest of Nam Island, the first deployable dry fuel hydrogen bomb developed by the United States. Its actual yield (15 MT) was 2.5 times its predicted, and the blast evaporated the underlying reef, two islets, and part of a third island (Nam). The resulting crater measured 2 km in diameter and 80 m deep (Figures 11a–c). The blast was accompanied by intense super-heated air and contaminated debris that rose more than 35 km that may have contributed to stratospheric wind shift from northward to eastward that led to the radioactive fallout over a broad area up to 300 km from the blast. The fallout rained down on five other atolls (uninhabited Eniwetok, Rongerik, and Ailinginae and inhabited Rongelap, Utrik), and also





**Bikini Atoll, Marshall Islands, Figure 11** Northwest rim of Bikini Atoll before and after the hydrogen bomb test Bravo at Bikini Atoll in 1954: (a) Pre-test view of Nam and two islands to the west (source: unpublished U.S. government map, circa 1947). (b) Post-test (1978) aerial photo view of the same scene showing Bravo Crater, damaged Nam Island, disappearance of two other islets to the west, and scour trenches along the north face of the crater (source: EG&G Electronics 1978; see Tipton and Meibaum 1981). Post test (2005) view of the same scene showing coralline algae recovery on the northern reef rim, including a 1 km scale bar at top of aerial photo [after Google Earth, Digital Globe and the U.S. National Aeronautical and Space Administration (NASA)].

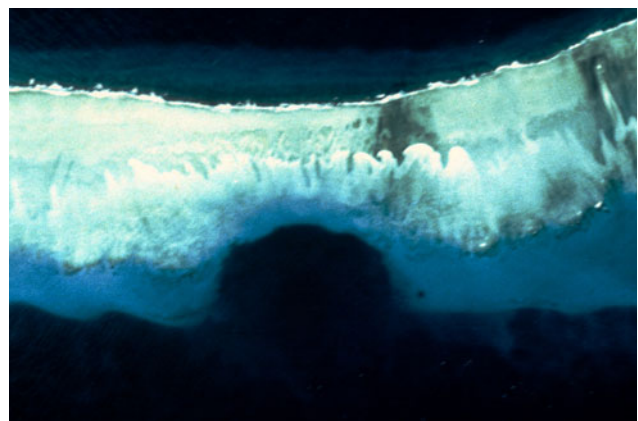
contaminated a Japanese fishing boat (*Daigo Fukuryū-Maru*) that resulted in one death. Although the afflicted atoll inhabitants were quickly evacuated after the blast, many later suffered from radiation sickness. During the subsequent half century, corals and anemones have recolonized Bravo Crater, and crustose coralline algae are now evident on the reef flats scoured, trenched, and fractured by the 1954 blast (Figure 11c). During Operation Redwing in 1956, several other barge-placed bombs of lesser yield (3.5–5 MT) were detonated in the north and northeast lagoon, and another surface test was detonated at the south crater site near Enemaan I. The northern test, Tewa (5 MT), created a large half crater along the north rim (Figure 12).

International pressure for a moratorium on atmospheric nuclear testing led to a final flurry of eight U.S. tests, including three fizzles, under Operation Hardtack in 1958 at Bikini. These included one large test (Poplar, 9.3 MT) and four smaller tests in Bravo Crater, and three smaller tests conducted in Enemaan Crater (Figure 13). The U.S. signing of the Partial Test Ban Treaty of 1963 ended all further underwater and atmospheric testing by the United States and other signatory nations. Since 1956 at least \$759 million has been paid to Marshall Islands, and \$15.3 million paid to Japan following the Bravo accident.

### Early cultural history

Extensive archaeological surveys in 1984–1987 included testing and dating at Bikini Atoll and revealed that:

- Eneu Island may have been settled more than 2,000 years BP
- Bikini Island may have been occupied beginning between 3890 and 1960 years BP, and
- Bikini Island may have been continuously occupied from 600 years BP



**Bikini Atoll, Marshall Islands, Figure 12** Aerial photo view (1978) of the Tewa 1956 bomb crater along the northeast rim of Bikini Atoll (source: EG&G Electronics in Tipton and Meibaum 1981).





**Bikini Atoll, Marshall Islands, Figure 13** Aerial photo view (1978) of the Enemaan Crater (southeast rim of Bikini Atoll) created by several nuclear tests at Bikini from 1956 to 1958 (source: EG&G Electronics in Tipton and Meibaum 1981).

The first two of these findings are still among the oldest cultural dates yet reported for Micronesia outside the Mariana Islands. The Bikini evidence relied on 18 radiocarbon dates, 58 confirmed indigenous artifacts, and several post holes and charcoal pits from an ancient village site eroding at one of the atoll shorelines. Moreover, the Marshallese legends and stories are consistent with the archaeological evidence and suggest that people began inhabiting the archipelago 2,000–3,500 years ago. Bikini oral history suggests that a chief (*iroij*) and his people first traveled from Wotje Atoll to Rongelap Atoll with a later generation of the clan led by a chief Larkelon who eventually arrived at Bikini and displacing the then existing residents at the atoll. The modern Bikini people can still trace their lineage back to Larkelon. The Bikini people were known for their large ocean-going sailing canoes and ability to travel and navigate over long distances. Similar to the situation with the Enewetak people, the Bikini people were sufficiently isolated and independent from other inhabited atolls and not subject to the rule of higher chiefs (*Iroij laplap*) until the last century. The early residents were also able to gain sufficient sustenance from the land and sea to maintain their culture over many centuries, and enhancing their independence and isolation.

### Recent history

The Spanish explorer Saaverda and his ship *Florida* in 1528 is credited as the first westerner to make contact with the residents of “Los Jardines,” either Bikini or Enewetak atoll. Although English explorers visited several neighboring Marshall Islands in 1788, no other Europeans visited Bikini again for nearly four centuries until 1825, when the German explorer Otto von Kotzebue sighted Bikini from a distance and naming the atoll “Escholtz” after the ship’s surgeon in 1823. Another possible visit by a trading schooner at Bikini in 1834 led to a confrontation with local residents resulting in casualties on both

sides. In 1858, Chramtschenko, Kotzebue’s former lieutenant, returned to Bikini, entering the lagoon. German copra traders began visiting the Marshalls in the 1860s, and by 1885 Germany claimed the Marshalls, Marianas (except Guam), and Carolines as protectorates. The copra trade was concentrated in the southern and central Marshalls where rainfall and production was much higher. Although small scale copra trading occurred at Bikini, no Germans ever settled on the atoll, and the Bikini people maintained their isolation, customs, dialect, and self rule until the dawn of the twentieth century.

In 1908 a Marshallese pastor arrived to establish the first Christian mission at Bikini. In 1914, Japan seized the Marshalls from Germany after the outbreak of WWI and retained them after Germany’s defeat, via a League of Nations Mandate in 1919. Japan promoted trade and development until the early 1930s but then closed the Marshalls and their other Pacific territories to outsiders and began fortifying many of the atolls, in violation of the earlier Mandate. During WWII, many residents of Bikini became indentured laborers assisting Japanese troops at Bikini who constructed a watchtower to guard against a possible American invasion. Young male residents were later sent to other islands to assist in the construction of other garrisons. Bikini continued to serve as an outpost during the remainder of the war. After the Pacific war ended in 1945, the United States assumed control of the Marshall Islands. In 1947, the new United Nations formalized U.S. custody of the Marshall, Caroline, and Mariana archipelagos as the Trust Territory of the Pacific Islands (TTPI). The overall goal of the arrangement was to prepare the peoples of the TTPI for self government. However, in March 1946, the U.S. planned to use of Bikini and Enewetak Atolls as part of the new Pacific Proving Ground for nuclear weapons testing.

### The nuclear nomads of Bikini

Commodore Ben H. Wyatt, military governor of the Marshalls District, reached agreement with the leaders of the Bikini People to use Bikini “for the good of mankind and to end all world wars.” As a result, the Bikini People were required to leave their home atoll and were moved to uninhabited Rongerik Atoll, to the east of inhabited Rongelap Atoll. Rongerik was small, exposed to heavy seas, and provided insufficient food for the new residents, and in 1948, the Bikini People were evacuated again to a tent city on Kwajalein Atoll until a permanent settlement site could be found. Eventually, the Bikini People chose to settle on Kili, a small single island in the southern Marshalls lacking a lagoon, a protective anchorage, and ocean access during seasons and periods of heavy seas. However, the island was favored by the settlers because it was not under the rule of any paramount chief and was uninhabited. Eventually, Kili was viewed as a prison, due to limitations on ocean access, inhabitants highly dependent on outside canned food and other essentials, and irregular visits by supply ships during heavy weather. At times, emergencies required air drops of food and vital supplies.

In 1967, after numerous radiological surveys at Bikini, the U.S. Atomic Energy Commission (AEC) concluded that Bikini was safe for re-habitation, and in 1968 President Johnson ordered the rehabilitation of Bikini. However, the Bikini Council visited Bikini and later decided against returning there due to concerns over the contamination of coconut crabs and other radiological safety hazards, but the leadership allowed individual families to choose for themselves. Three extended families and about 50 other Marshallese workers opted to return to Bikini Island in 1969. The rest of the 540 People of Bikini remained at Kili. After 5 years the population at Bikini had grown to 100. The U.S. continued efforts to cleanup the atoll, construct housing, replant coconut trees, move off all military and AEC personnel, and discontinue regular air service to Bikini by late 1972.

However, several U.S. agencies warned of “higher levels of radioactivity than originally thought” . . . “Bikini appears to be hotter or questionable as to safety” . . . and the “groundwater was too contaminated to be consumed as drinking water.” Later AEC scientists revealed that locally grown foods, especially coconuts, pandanus, breadfruit, and coconut crabs bio-accumulate hazardous radio-nuclides including Cesium<sup>137</sup> and Strontium<sup>90</sup>. Later medical tests of the islanders revealed low levels of Plutonium<sup>239</sup> and Plutonium<sup>240</sup>, radio-nuclides with half lives of thousands of years. Confused by the reports provided by the U.S., the Bikini People filed suit in federal court demanding the U.S. to complete a scientific survey of Bikini and the other northern Marshall Islands. In 1978, the U.S. agreed to accomplish an aerial radiological survey of the Northern Marshalls. Unaware of the extent of the radiological danger, the settlers opted to remain on Bikini Island until the studies were completed. However, by May 1977, levels of Strontium<sup>90</sup> in the well water exceeded the maximum U.S. limits, and a month later another study revealed that “all living patterns involving Bikini Island exceeded federal guidelines for 30 year population doses.” Moreover, U.S. scientists recorded a major increase in Cesium<sup>137</sup> body burdens in the majority of the people living on Bikini I. Alarmed by these findings, the U.S. Department of Interior (DOI) advised the settlers to limit consumption of one coconut per day and to begin shipping in food from outside the atoll. However, in April 1978 medical examination of the islanders revealed that radiation levels were well above the maximum permissible level in many of the 139 people on Bikini, and by May 1978, DOI described the 75% increase in Cesium<sup>137</sup> as “incredible.” Hence, all islanders at Bikini were evacuated to Ejit Island on Majuro Atoll in September 1978, where the community remains to this day. Meanwhile, the main population of the Bikini people continues to live on Kili Island.

### Restoration for resettlement

Over the next 3 decades, the U.S. evaluated various options for the safe return of the Bikini People to their home atoll. Lawrence Livermore and Brookhaven National Laboratories

assessed the physical options and maintained medical support for all people exposed to radiation. Distrustful of U.S. Government Agencies and Laboratories, the Bikini People petitioned the U.S. Congress to fund independent bodies to evaluate and advise them on the pros and cons of various options to restore Bikini for the safe return and habitation at Bikini Atoll. The first of these was the Bikini Atoll Rehabilitation Committee (BARC) consisting of several highly regarded scientists and engineers in the fields of medicine, radiation, physics, engineering, soils, and agriculture, and the present writer served as the environmental specialist for BARC from 1984 to 1987. BARC concluded that habilitation of Bikini Island’s groundwater to potable levels was not possible and suggested a smaller permanent settlement at Eneu Island where the environment is free of radiological contamination. As for safe resettlement options at Bikini Island, BARC proposed four doable options:

- Removing all topsoil from Bikini Island and possibly replacing it with clean soil
- Saturating the soil with fertilizer containing potassium, an element of similar properties to radioactive cesium and strontium that would be preferentially taken up by crops
- Soak the soil with seawater which has abundant sodium that would block the uptake of radioactive cesium and strontium, but would render the soil unusable for agriculture
- Buy land with reparations funds from the U.S. Nuclear Claims Tribunal and live somewhere else until Bikini’s radioactive cesium and strontium decay to safe levels: the two radio-nuclides have half lives of 28–30 years, meaning the soil would be safe within two to three centuries

In the 1990s, the Bikini People hired their own advisors and have recently solicited the advice of the International Atomic Energy Agency for evaluation and advice. However, the People of Bikini have not accepted or pursued any permanent alternative to this date. The one exception was opening up the atoll to small-scale sport and technical diving over the past decade. The sunken shipwrecks, bomb craters and the prolific recovery of the coral reefs from past insults are attractions of major interest to many visitors.

### Summary and conclusions

Under present circumstances, it is uncertain that the Bikini People will soon return to Bikini Atoll. The 63 years that have passed since the residents were first removed from the atoll have instead led to the passing of most of the original residents. Only a few of the present Bikini population that now totals more than a thousand have spent much time or lived at Bikini. All are now a part of a vastly different socio-economic age and culture. Should a larger group of the Bikini People return to the atoll when it is again “safe,” global climate change may have already washed away some of the islands and any hope of resorting

a subsistence live style practiced by the former inhabitants. Perhaps, this may be the end of a chapter in human history where a small society was able to sustain itself and endure the rigors of nature and mankind for over several millennia, perhaps, among the longest any society has ever survived in a small space during this modern era of civilized humanity. In January 2009, the Kili-Bikini-Ejit Local Government and the Republic of the Marshall Islands nominated Bikini Atoll for World Heritage in early 2009. By the end of 2010, the World Heritage Committee will make its recommendation on whether the atoll will be inscribed as a World Heritage property.

### Current investigations, controversies, and gaps in current knowledge

Although much has been published about the people and the impacts caused by the nuclear testing in Bikini, there has been very little rigorous scientific research focused on the degree to which the coral reefs of Bikini have recovered after the 1950s. Buddemeier et al. (1974) sectioned the skeletons of corals that lived before and after the nuclear test era at neighboring Enewetak. Although comparable specimens were not collected at Bikini, the Enewetak results showed no evidence of consistent differences in growth rate in the annual band widths laid down by individual corals before and after the nuclear testing era. Moreover, Agegian et al. (1987), the present writer, and Richards et al. (2008) report many large coral heads thrive on Bravo Crater and virtually all pinnacles and patch reefs in the lagoon (Figure 14) and in the adjacent Nam Island rock quarry (Figure 15), where one large coral must have settled and began growing shortly after the Bravo test.

Richards et al. (2008) maintain that at least 28 species reported by Wells (1954b) before most of the nuclear tests “represent genuine losses” attributed to the nuclear testing program. This was based on comparisons of Wells species before the tests and the Richards team list 42 years after the final test. However, Richards implicitly assumes that both investigators accounted for all the species present at the atoll at the time of the surveys. Moreover, they did not consider the unpublished coral surveys of Maragos (1985) who reported 17 of the lost species at Bikini in 1985. More importantly, 49 species from Wells (1954b), 22 species from Maragos (1985), and 50 species from Richards et al. (2008) were not reported by the other respective investigators. The most likely explanation is that the “losses” is the incomplete compilation of all species by any of the three investigators. In fact, the Wells compilations were primarily based on deep water dredged hauls to depths of more than 60 m and shallower reef collections. In contrast, the other two investigators relied on scuba surveys at depths which were not readily accessible at the time of the Wells surveys. Moreover, many of the Wells-only species occur in deep water that could have only been collected by dredged hauls. Compiling all lists together and developing species accumulation curves for



**Bikini Atoll, Marshall Islands, Figure 14** View of top of pinnacle in eastern Bikini lagoon in 1985 showing luxuriant development of stony corals (*Acropora* spp.) 27 years after the termination of nuclear tests at the atoll (source: J.E. Maragos).



**Bikini Atoll, Marshall Islands, Figure 15** View of 1984 hemispherical coral head (2 m diameter) of *Porites lutea* that settled and grew in the rock quarry near Nam Island after the 1954 Bravo Test. Ground zero for the test was approximately 1.5 km from the quarry (source: J.E. Maragos).

the 29 Maragos (1985) sites reveal that the total list is still incomplete, and that there may be as many as 304 stony coral species based on bootstrap estimates.

Regardless, the coral reefs of Bikini Atoll deserve continuing analysis of their response and recovery from the



nuclear era and their prognosis during the global climate change of the future. Especially important is to continuing the monitoring of radio-nuclides in marine food webs and monitoring the abundance and distribution of reef biota at fixed sites over extended time. Such studies would likely benefit the future use and occupation, if any, by present and future generations of the Bikini People.

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## Cross-references

Algae, Coralline  
Atoll Islands (Motu)  
Atolls  
Eniwetok Atoll, Marshall Islands  
Foraminifera  
Geomorphic Zonation  
Lagoon Circulation  
Mururoa Atoll  
Pacific Coral Reefs: An Introduction  
Patch Reefs: Lidar Morphometric Analysis  
Reef Drilling  
Reef Flats  
Reef Structure  
Spurs and Grooves  
Wave Set-Up  
Waves and Wave-Driven Currents

need firm substrates on which to settle. Binding and encrusting organisms such as encrusting sponges (Knott et al., 2006; Turon et al., 1998), foraminifers (Machado and Moraes, 2002; Perrin, 2009), or algae stabilize the loose carbonate grains and thus cement the reef body. The most important encrusting organisms of modern reefs are the light-dependent calcareous red algae (known also as coralline algae), but many other calcareous encrusting organisms exist including polychaetes, phoronid worms, chaetognaths (arrow worms), holothurianschordates (ascidians), foraminifera, corals, bivalves, algae, and bryozoans. These organisms bind sedimentary particles to create a living framework or shelter or the binding process is purely a by-product of the organisms' digestion and scavenging of the sedimentary environment for food. Although in most modern reefal environments, binding organisms are in the minority, they were responsible for building entire bioherms or reef systems in the geological past and thus during certain eras, binding organisms were much more widespread and common than today. However, even in modern times, binding organisms are critically important as they contribute calcium carbonates to the reef framework (Bianchi et al., 1995; Logan, 1961; Mallela, 2007; Perry, 2000), bind particles and rubble and thus stabilize the substrate (Fischer et al., 2000; Krasnow and Taghon, 1997; Rasmussen et al., 1993; Rasser and Riegl, 2002), and promote larval recruits and offer nutrients and habitats for other species such as bacteria, algae, and foraminifera (Davies et al., 1992, 1998; Maneveldt et al., 2006; Riemann and Helmke, 2002).

Duration of binding depends on several factors and few data are available. Preliminary stabilization by seagrass, uncalcified algae, or sponges may be rapid due to their fast growth, but these preliminary stabilizations last only 1 month to a few months (Rasser and Riegl, 2002), whilst rigid binding by encrusting coralline algae can take place within seven months. Interlocking of branched coralline algal crusts may take place within a few years, or within 1 year, depending on the growth rates of the particular species. In addition, binding activity that contributes to rapid encrusting and cementation is approximately double in fore-reef settings than in back-reef settings (Perry, 1999; Rasser and Riegl, 2002).

## Algal structures

Reefal environments contain many different algal communities pertinent to binding and accreting carbonate material. Algae form intricate growth patterns and species are often overlapping such as encrusting red algae or blue-green boring and epiphytic algae (Dean and Eggleston, 1975). The distribution and growth of these and other encrusting organisms depend on factors such as environment (fore reef, lagoon, etc.), substrate composition (soft sediments, corals, etc.), water depth and temperature, light level, turbidity, wave and current energy, and sediment influx (Mallela, 2007; Perry, 2000; Rasser and Riegl, 2002). Some encrusting algae commonly grow around

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## BINDING ORGANISMS

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## Definition and introduction

Coral reef environments host many organisms that actively precipitate mineral matter and encrust or bind sedimentary particles together. In reef systems, waves, storms, and boring organisms constantly produce loose material (mostly skeletal debris), but reef organisms often

a nucleus (coral rubble, shell fragment, etc.) to form rhodoliths. These are common in reefal environments and growth rates of  $\sim 1.6$  mm/year have been determined (Ballantine et al., 2000), although much slower growth rates have also been suggested. In the Caribbean, filamentous algae are estimated to produce  $700 \text{ g C/m}^2/\text{year}$  and macroalgae  $1,170 \text{ g C/m}^2/\text{year}$  (Rasser and Riegl, 2002), whilst a study from Jamaica determined the carbonate production of coralline algae using artificial tiles to be between  $70$  and  $150 \text{ g/m}^2/\text{year}$  (Mallela, 2007).

Modern reefal environments contain abundant algal material but only few of those form mats and biofilms, which trap, bind, and cement sedimentary material and form accretionary structures. These binding structures of which the finer-bound matrix is preserved, called stromatolites, dominated the shallow shelves during early Earth (Allwood et al., 2006; Grotzinger and Knoll, 1999). At present, shallow marine stromatolites occur around the world but are often very limited in extent. The most famous modern stromatolite occurrences are in Shark Bay (Western Australia) (Logan, 1961), Lagoa Salgada (Brazil) (Lemos et al., 1994), Highborne Cay and Exuma Sound (Bahamas) (Dill et al., 1986; Dravis, 1983), Teikehau Atoll (French Polynesia), Chetumal Bay (Belize), etc. These structures are covered with biofilms of microorganisms (in Shark Bay  $\sim 90\%$  cyanobacteria and  $10\%$  archaea), which trap, bind, and cement sedimentary particles. Early work from Shark Bay showed that two major types of stromatolites exist: (1) the eualgal-cyanobacterial stromatolites (generally coarse grained) and (2) the cyanobacterial stromatolites (fine grained) (Awramik and Riding, 1988). There, the algal eukaryotes produce subtidal columnar stromatolites due to their extracellular gel formation, which trap and bind sediment and biogenic fragments (e.g., ooids, mollusks, diatoms). Similarly, the stromatolites from Exuma Sound (Bahamas) are also coarse grained with dasyclads and cyanobacteria, which trap sands that are then bound and cemented by acicular aragonite and chasmolithic green algae (Dravis, 1983). More recent investigations into the microorganisms associated with stromatolites demonstrated a uniquely high diverse community of cyanobacteria, bacteria, and archaea (Burns et al., 2004).

## Polychaetes

Sedentary polychaetes, including serpulids, sabellariids, and sabellids, are another important encrusting group of organisms. Most polychaetes have a tube constructed by sediment particles and mucus (organic compounds), in which they live or grow erect attached to each other, which may form large aggregates. The branchial crown of sabellids functions both in respiration and in the collection of suspended particulate matter from the surrounding water (Bonar, 1972). The tube formation is a consequence of burrowing as sand particles adhere to the mucous sheets secreted by the mucous cells of the epidermis. The first portion built of the tube is a small, transparent mucous

cylinder, about 2-mm long (Kirtley, 1994). The worms collect small fragments of minerals, diatom frustules, sponge spicules, and other small objects of manageable size and implant these reinforcements in the delicate mucus. Later in their tube building, the worms choose among a greater variety of materials. Into upper parts of the cylinder are set angular quartz grains, small fragments of broken mollusk shells, fecal pellets, and other materials – all arranged in an overlapping spiral pattern that rises to the base of the flared opening. Tube formation and growth of 2.5–5 cm may occur within 2 months (Naylor and Viles, 2000) and the tube particle sizes are often coarser than the mean particle size of surrounding sand. In addition, flat, platy and elongate particles are preferentially used. A study from Florida showed that most sand particles ranged between 0.25 and 0.5 mm (Main and Nelson, 1988). In the Caribbean, analysis of modern polychaete worm tubes showed distinct micritic peloidal lamellae morphologies (Fischer et al., 2000). Histological investigation of the tubes of *Dodecaceria* showed that the tube formation is related to two processes. The initial process is weakly controlled by the worm itself (matrix mediated). The worm produces acidic organic mucus substances, which are enriched between the soft tissue and the tube wall. The mucus has an antifouling capability and inhibits the mineralization of the mucus for a certain time. Within polychaete tubes, the mineralization events of the mucus are responsible for the stromatolitic microfabric of the tubes. Within the spaces between the primary lamellae, nonspecific extracellular polymeric substances-rich mucus is enriched, which controls the formation of fibrous aragonitic crystals and peloidal fabrics. Hence, the mucus plays an important role during the organomineralization process, which is not controlled directly by the organism (Fischer et al., 2000).

Sabellariid reefs flourish best where vigorous wave and current action cause the suspension and transport of sand-size particles (Kirtley, 1994). In some areas (e.g., east and northeast Brazil and southwest India), sabellariid reefs may extend laterally for thousands of kilometers along the shores of modern seas (Pandolfi et al., 1998). The sabellariids occur in densities as many as 15,000–60,000 individuals/m<sup>2</sup> and are known to have life spans as long as 10½ years (Kirtley, 1994). Aggregations of sabellariid worms create geological formations called worm reefs (Main and Nelson, 1988) and have been reported from around the globe, including Europe (Kirtley, 1992; Naylor and Viles, 2000), Taiwan (Chen and Dai, 2009), Hawaii (Pandolfi et al., 1998), Fiji (Bailey-Brock et al., 2009), etc.

## Summary and conclusion

Coral reef environments host many organisms that actively precipitate mineral matter, encrust or bind sedimentary particles together. The binding organisms of modern reefal ecosystems are critically important as they contribute calcium carbonates to the reef framework, bind particles and rubble and thus stabilize the substrate, and



promote larval recruits and offer food and nutrients as well as habitats for other species such as bacteria, algae, and foraminifera. The most important encrusting organisms of modern reefs are the light-dependent calcareous coralline algae, but many other calcareous encrusting organisms exist including polychaetes, phoronid worms, chaetognaths, holothurians, chordates, foraminifera, corals, bivalves, algae, and bryozoans. These organisms bind sedimentary particles to create a living framework or shelter or the binding process is purely a by-product of the organisms' digestion and scavenging of the sedimentary environment for food.

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## Cross-references

[Algae, Coralline](#)  
[Aragonite](#)  
[Bindstone](#)  
[Bioherms and Biostromes](#)  
[Bryozoa](#)  
[Calcite](#)  
[Coral Reef, Definition](#)  
[Devonian Reef Complexes of the Canning Basin](#)  
[Foraminifera](#)  
[Fossil Coralline Algae](#)  
[Molluscs](#)  
[Permian Capitan Reef System](#)  
[Reefal Microbial Crusts](#)  
[Rhodoliths](#)  
[Seagrasses](#)  
[Sponges](#)  
[Stromatolites](#)  
[Submarine Lithification](#)

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## BINDSTONE

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Bindstone is a modification proposed by Embry and Klován (1971) to the Dunham (1962) Boundstone type of limestone where the framework organisms were encrusting and binding the sediment.

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## Cross-references

[Classification of Carbonates](#)

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## BIOEROSION

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## Definition

Bioerosion can be defined as the destruction and removal of consolidated mineral or lithic substrate by the direct action of organisms (Neumann, 1966) and is complemented by physical and chemical processes of erosion. This review deals only with the removal of substrate from coral reefs and concentrates on modern day reefs. However, there

is an extensive literature on boring organisms on fossil reefs, for a review see Tapanila (2008) and the agents and mechanisms of boring seem similar on these reefs to those occurring on modern day reefs (Wood, 1999).

## Introduction

Bioerosion is a natural process occurring on all reefs although rates and agents may vary across the reef and together with reef growth which also varies, results in them being dynamic systems. It is the balance between these two processes which determines the overall shape of the reef together with physical and chemical erosion of the coral substrate. Bioerosion includes the removal of surface substrate by grazing organism (*Acanthaster planci*; *Sponges*) and the loss of substrate by boring organisms which produces a continual supply of lagoonal and inter-reefal sediments. While reef growth has been well studied (Barnes and Chalker, 1990), bioerosion has been relatively poorly studied. Although this situation is likely to be rectified, as reefs are increasingly being impacted by anthropogenic effects, which often results in changes in the balance between rates of reef growth and reef destruction, with the latter far exceeding reef growth in many parts of the world (Pari et al., 2002; Sheppard et al., 2002). This loss of substrate may have severe biological, economic, and social consequences each of which will be discussed later.

A wide range of organisms are capable of boring into coral substrate and this includes both macro and microborers with recruitment via pelagic larvae or propagules (McCloskey, 1970). Reef building corals have a thin veneer of living coral polyps over the coral skeleton, and these are active carnivores and can capture any larvae of borers which settle on them using their nematocysts. Larvae can also become trapped in the ciliary feeding currents generated by the polyps and carried to the mouth and eaten. This ensures that few larvae settle on live polyps, instead they settle on damaged polyps or any dead areas of the colony or at the base of the colony where typically there is no veneer of living coral. However, once the colony dies, for example, as a result of disease (Sussman et al., 2008), bleaching (Pratchett et al., 2008), predation by Crown of Thorns starfish (*Acanthaster planci*) (DeVantier and Done, 2007), the gastropod mollusc *Drupella* spp., (Morton and Blackmore, 2009), or by other coral predators (Rotjan, and Lewis, 2008), or from the effects of storms (López-Victoria and Zea, 2004), the substrate is rapidly colonized by microborers which conditions the surface and facilitates recruitment of a suite of macroborers.

## Microborers

### Components and processes

A diverse array of micro-organisms colonize coral substrates including cyanobacteria, algae, and fungi; for a review of their taxonomy, see Kobluk and Kahle (1977) and for a review of their boring activity, see Tribollet

(2008). They consist of boring autotrophic and heterotrophic microorganisms or euendoliths (boring microflora) which actively penetrate (biochemical dissolution) the coral substrate (Golubic et al., 1981). Species composition of these communities varies between live and dead substrates. The species composition of those occurring in live coral is positively phototrophic, fast growing taxa which can keep up with accretion of the coral, and can stay in the surface layers of the substrate to obtain sufficient light for their growth (Tribollet and Payri, 2001). One species of chlorophyte *Ostreobium quekettii* Bornet and Flahault, 1899, has been recorded widely from Atlantic and Pacific corals but this may represent a suite of cryptic species (pers. comm. H. Verbruggen as cited in Tribollet, 2008). These algae form a distinct green band just below the coral surface (Figure 1a). Infestation occurs as the coral polyp is settling on the substrate and beginning to lay down a coral skeleton. The same suite of microborers also colonize encrusting coralline algae growing over dead coral substrates. Following death of the coral colony another suite of algae colonize the substrate within a few days (Hutchings, 1986; Gektidis, 1999) (Figure 1b). Early colonists are short-lived opportunistic species. Within 6–12 months, these endolithic algal communities become dominated by low-light specialists and heterotrophic fungi, and are referred to as “mature communities” (Tribollet, 2007). Such changes in species composition are driven by reduced light penetration as the surface of the substrate becomes covered with epilithic organisms, which reduces the amount of light able to penetrate into the substrate and therefore species which can utilize these lower levels flourish. The species composition of the epilithic biota strongly influences which species of boring microflora (euendoliths) are present. For example, under turf algae (Figure 1b) growing on dead *Porites*, colonies of the cyanobacteria *Mastigocoleus testarum* are abundant, whereas a different suite occurs under crustose coralline algae (Chazottes et al., 2002). Substrates in turbid areas may be covered with sediment which inhibits or reduces the density of boring microflora (Osorno et al., 2005).

### Method by which microborers bore

It was thought that the boring microflora penetrated the substrate by dissolving its crystalline matrix (Tudhope and Risk, 1985), but recent studies suggest that there is a temporal separation between photosynthesis and boring activities (Garcia-Pichel, 2006). This involves active transport of  $\text{Ca}^{2+}$  from the apical cell of the filaments to their trailing end occurs which would make dissolution of the substrate around the apical cell feasible when interstitial pH is high due to photosynthesis. This may explain why micrite and brucite are commonly seen precipitated around the microflora filaments at the surface of dead substrates (Kobluk and Risk, 1977). But more studies are required and it may be that the process of substrate dissolution varies depending on the taxa, type of substrate, and environmental conditions (Tribollet, 2008).

## Macroborers

### Polychaetes

#### *Diversity of polychaetes*

Representatives of a variety of polychaete families are found, including Eunicidae, Sabellidae, Spionidae, and Cirratulidae, which are not closely related, suggesting that the ability to bore into coral substrate has arisen several times. Even within a genus not all members are borers. In the Indo-Pacific, some species have been reported as having wide distributions, such as *Nematonereis unicornis* and *Lysidice collaris*, but this needs to be carefully checked using both morphological and molecular data. Information on the boring species present in the Caribbean is lacking. Boring polychaetes are primarily found in dead coral substrate, when they occur in live coral typically a few polyps have been damaged which presumably allows the larvae to settle and penetrate. The only exception to this appears to be a species of Flabelligeridae which is common in some live coral colonies in Hong Kong Harbour (Hutchings, pers. observ.).

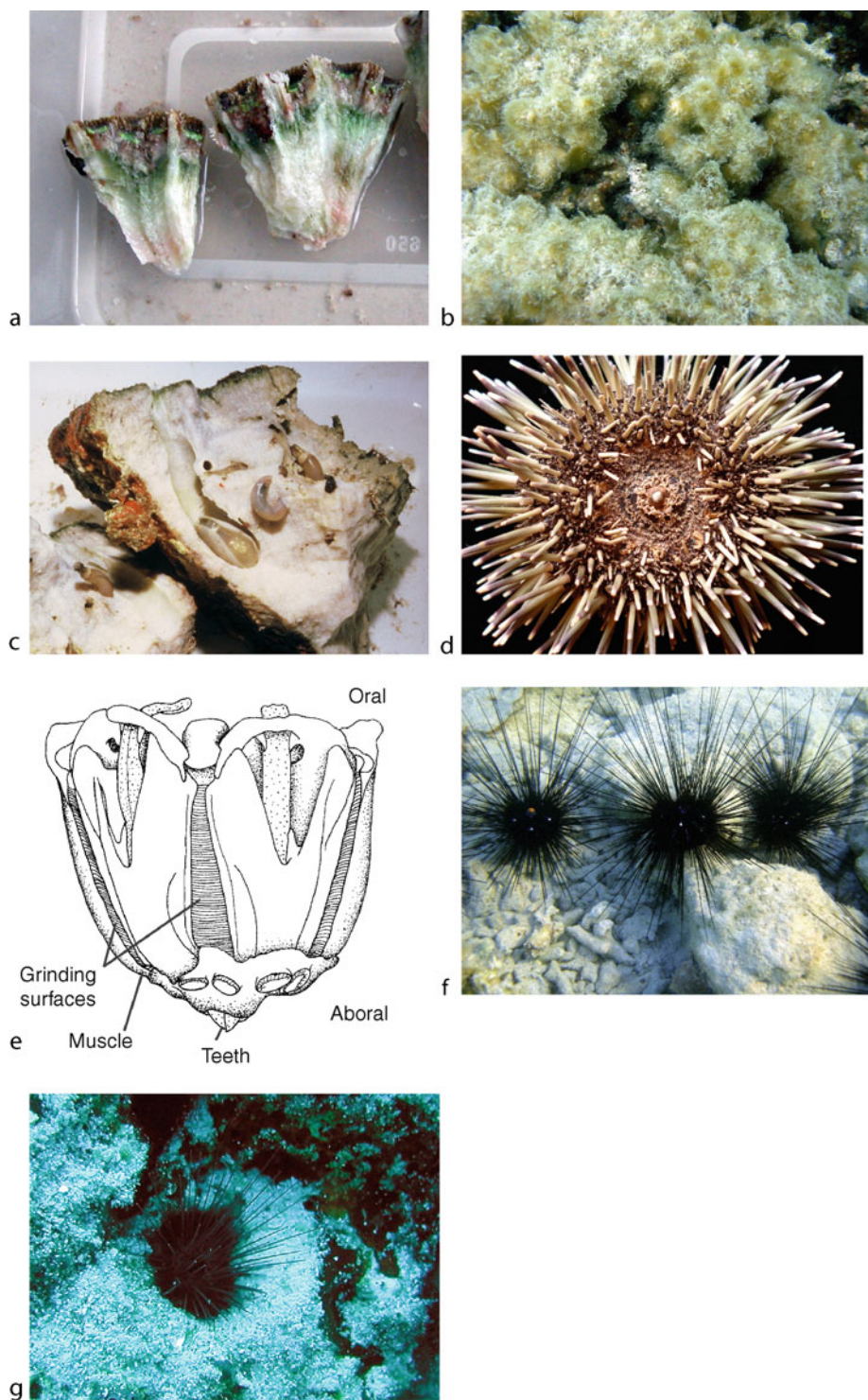
#### *Succession of polychaetes*

The first suite of macroborers to arrive are short-lived polychaetes such as species of *Polydora* (Spionidae) and Fabriciiniids (Sabellidae), which can be extremely abundant. These species are either deposit or filter feeders which feed on the sediment trapped in the irregularities of the surface of the substrate or spread their feeding crowns out into the water column above the surface where they filter out food particles. Obviously these species are susceptible to being removed when parrotfishes or echinoids graze on the substrate as they live in the surface layers. Over the next year or so, other boring organisms recruit to these substrates including a range of other longer lived polychaetes belonging to the families Cirratulidae, Eunicidae and Sabellidae (Hutchings et al., 1992; Pari et al., 1998, 2002) which exhibit a range of feeding strategies including surface deposit feeders, filter feeders and others are predators. One suspects that the predators feed on the other macroborers but some may be more opportunistic and also feed on the microborers.

#### *Recruitment of polychaetes*

Following successful colonization of newly available substrates by a suite of endolithic algae, viruses etc. and turf algae, pelagic larvae of boring polychaetes settle on the surface and turf algae may provide some protection for these larvae from small scale water movement which could wash them off the substrate as they metamorphose and begin to bore. Observations on experimental substrates suggest that larvae tend to settle in small depressions (Hutchings, pers. observ.). High rates of mortality of such larvae must occur at this time, but experimental studies have shown that some recruitment of this initial suite of polychaete macroborers occurs throughout the year and to all habitats (Hutchings et al., 1992; Kiene and





**Bioerosion, Figure 1** (a) Endolithic algae inhabit the skeletons of corals, living amongst the crystals and over time weakening the skeleton. (b) Dead coral substratum covered by turf algae (photo: O. Hoegh-Guldberg). (c) In situ dead coral habitat split open to reveal boring sipunculans and bivalves, burrow of boring bivalve (photo: P. Hutchings). (d) The grazing echinoid *Echinometra mathaei*, oral surface showing Aristotle's lantern partially protruding from the mouth that it uses to actually scrape off the surface of the coral (photo: A. Miskelly). (e) Diagram of Aristotle's lantern (Illustration after Anderson, 1996). (f) *Diadema setosum* a grazing echinoid linked to major erosion of western Indian Ocean reefs (photo: O. Hoegh-Guldberg). (g) *Echinostrephus* sp., sitting in its home scar that it has eroded (photo: O. Hoegh-Guldberg).

Hutchings, 1994a, b). However, maximum recruitment of this suite of polychaetes occurs during early summer (Hutchings and Murray, 1982) and significant variations occur between sites on a reef, with maximum recruitment of most species occurring on windward and reef flat sites, and least to a lagoonal patch reef (Hutchings et al., 1992). Studies over several years have shown that as well as seasonal and temporal variation there are also variations between years, and it is suggested that local weather patterns are critical in the dispersal of these larvae (Hutchings et al., 1992). Once the polychaetes are established within the substrate they must retain an opening to the exterior through which they obtain oxygenated water and their food, discharge their waste products and gametes. The only exception to this are some of the eunicids which develop modified back ends full of gametes which become detached from the rest of the body and leave the burrow and swim up into the water column to spawn on particular nights of the year. The most famous being the Palolo worm (*Eunice viridis*) (Caspers, 1984). So basically once the polychaetes have burrowed into the substrate they are effectively entombed and never leave except for some of the eunicids and then only posterior segments.

In addition to recruitment via pelagic larvae, members of the genus *Dodecaeria* (F. Cirratulidae) can also undergo asexual reproduction by splitting into individual segments and with each segment developing a new head and tail, and so inside the burrow an entire family group may be found.

#### *Mechanisms of boring by polychaetes*

Polychaetes bore into the substrate using either chemical secretion to dissolve the reef framework or perhaps mechanically grind the substrate or use a combination of these methods (Hutchings, 2008) but the precise details still need to be worked out. Some of the boring polychaetes such as sabellids and cirratulids must dissolve the substrate as they lack any structures with which to mechanically bore, and sabellids at least have well developed glandular areas at the base of the crown which may be responsible for secreting chemicals which dissolve the substrate. Other groups such as *Polydora* spp. (F. Spionidae) have thickened chaetae on segment 5, and it has been suggested that they can use these to grind the substrate. However, removal of these modified chaetae did not impede the burrowing capacity of *Polydora websteri* (Haigler, 1969). The same species boring into mollusc shells secretes a viscous fluid which dissolves the organic matrices of the shell and subsequently dissolves the exposed crystals (Zottoli and Carricker, 1974), but the chemical composition of this fluid was not determined. More recently it has been suggested that this fluid is secreted all along the body of the worm (Sato-Okushi and Okoshi, 1993) and presumably a similar fluid is secreted by other species which bore into coral substrate. Examination of the walls of the burrows of eunicids reveals bite marks which match the size of their well-developed jaws. Burrows of the larger polychaetes are

distinctive and can be recognized in sections of substrate and those of *Notaulux* (F. Sabellidae) are lined with a fine chitinous tube (Hutchings, 2008). Identifying the burrows of the smaller early recruiting polychaete species is far more difficult as their dimensions are similar to the porosity of the coral substrate.

## Molluscs

#### *Diversity of molluscs*

Representatives of six bivalve families are known to bore into coral (Figure 1c). Of these the Petricolidae, Pholadidae, and Clavagellidae are represented only by a few species and generally bore into dead coral substrate. Species of the Lithophaginae and the Gastrochaenidae play a major role in bioerosion of dead coral with the latter family the dominant one in both the Pacific and the Caribbean. Another suite of species bore into living coral belonging to the Mytilidae and some genera of Lithophaginae. Within *Lithophaga* some species are capable of living in a wide range of coral species, whereas others are restricted to a single species. Species of *Leptoconchus* and *Magilopsis* belonging to the gastropod family Coralliophilidae bore into living coral (Soliman, 1969).

The Indo-Pacific and Atlantic coral reef faunas are quite different, with only 7% overlap at the generic level but none at the species level, 24 genera have been recorded from the Atlantic and 87 in the Indo-Pacific. The genera which overlap are those containing species of the less specialized dead coral borers, and the other genera including those which bore into live coral evolved as the corals themselves diversified (Rosen, 1984). For more information on the evolution of boring bivalves and a detailed list of the coral species bored by particular species of bivalves see Morton (1990).

#### *Succession of molluscs*

Experimental substrates have rarely been exposed for long enough to demonstrate if any succession of species occurs as the dead substrate ages. Obviously as the surface of the dead substrate is eroded the bivalve has to continue to bore deeper in the habitat whereas those boring into live coral must reverse their direction of their boring as the coral grows upwards enlarging its burrow posteriorly to keep the entrance above open, and in these lithophagids, posterior pallial glands secrete an active chelating agent (Morton, 1990).

#### *Recruitment of molluscs*

Bivalves recruit via pelagic larvae, and Morton (1990) suggests that those recruiting to dead coral substrate are similar to other bivalve larvae in their ability to find a suitable substrate on which to settle and bore. Whereas larvae of species recruiting to live corals have to have special adaptations. It appears that larvae settling inadvertently onto a coral species, which they do not normally bore into, are stung by the coral nematocysts and rapidly withdraw their feet. Whereas larvae settling on a coral species which

they are found to bore into, can stay on the surface of the coral for days until they settle and bore into the coral. Scott (1988) found that the larvae enter the coral via the coelenteron and she suggests that they then undergo metamorphosis and eventually bore through the walls into the skeleton although she did not actually observe this. This suggests that the larvae have morphological and behavioral specializations so as to select their specific coral species host and to penetrate its defences.

#### *Mechanism of boring by molluscs*

Many early studies (e.g., Yonge, 1963; Soliman, 1971) suggested that boring in bivalves was largely mechanical but more recent studies of species of Lithophaginae, Pholadidae, and Tridacnidae which bore into live coral suggest that they are chemical borers, with acid-like secretions being produced by the mantle folds. In the species of Lithophaginae which bore into dead coral, calcium carbonate is used to smooth and fill the boring anteriorly. In those more specialized species which bore into live coral the calcium is used to smooth and fill the boring posteriorly and to form secondary extensions to the shell for predator defence. The secretions are produced in this group by pallial glands located in the middle folds of the mantle of lithophagids and in other groups the boring glands are in the inner folds around the pedal gape. Morton (1990) provides more details on selected species across the families as well as details of the structure of the tubes which can be easily assigned to particular species. Detailed descriptions and illustrations of some boring bivalves from the Maldivian coral reefs are given by Kleeman (2008). Morton (1990) suggests that in live coral borers over geological time have evolved from mechanically boring ancestors toward chemical erosion and selective relining of the burrow so that the occupant fits snugly within it.

Bivalves living in live coral have glands on their siphons which secrete a substance which either inhibits nematocyst discharge or protects the siphons from them. Species living in dead coral do not possess these glands (Morton and Scott, 1980). But all boring species living in either dead or live coral need to protect their siphons from predation by predatory animals moving over the surface of the substrate. Some species decorate the openings of the siphon with detrital fragments, others can retract their siphons back down the neck of the burrow and other species protect the posterior edges of the shells valves to help minimize predation. For more details see Morton (1990).

#### *Fossil record of molluscs*

Boring bivalves are well represented in the fossil record, and some of these ancient bivalves are almost certainly ancestors of modern borers, they were uniformly circumtropical in distribution and primarily borers of dead coral. Only in recent times with the evolution of modern coral reefs was the close relationship between boring bivalves and live coral really established, together with the strong separation of Atlantic and Indo-Pacific fauna.

## Sipunculans

### *Diversity of sipunculans*

A number of species bore into coral reef substrates and coral rubble representing several genera. In a study of the distribution of sipunculans at Carrie Bow Cay, Belize, Rice, and Macintyre (1982) found eight species, of which six inhabited burrows within the coral substrate and two which were found on crevices and crannies. Several genera were represented including *Lithacrosiphon*, *Aspidosiphon*, *Paraspidosiphon*, and *Phascolosoma*. Similar genera were recorded from coral substrates in French Polynesia with some additional ones, but they were not all identified to species (Hutchings and Peyrot-Clausade, 2002). Eight species were recorded from studies along a transect in North Queensland, and two species were shared between the Caribbean and the Great Barrier Reef, *Paraspidosiphon steenstrupii* and *Phascolosoma perlucens* (Osomo et al., 2005) (Figure 1c). As with the polychaetes, the habit of boring appears to have arisen independently in several families of sipunculans and the so called widely distributed species need to be carefully checked using morphological and molecular techniques.

### *Succession of sipunculans*

Rice and Macintyre (1982), working in Belize, found that sipunculan density was greatest in relatively unaltered coral substrate which had relatively little secondary infill of calcite cement and that the corals with uniform skeletal framework like *Porites* and *Acropora* were favoured. They found that highly eroded rocks of coral substrate contained few if any sipunculans. Experimental studies have clearly shown that sipunculans do not appear initially but have not revealed any distinct patterns of succession, only that individuals increase with size with increasing exposure (Hutchings and Peyrot-Clausade, 2002).

### *Recruitment of sipunculans*

Rice and Macintyre (1982) have shown that the species of sipunculans which recruit depends on the time of year as individual species have different breeding seasons. On the Great Barrier Reef, Hutchings et al. (1992) found that sipunculans exhibited spatial and temporal variations in recruitment, with some years better than others, and that recruitment was almost totally restricted to summer months, suggesting that breeding occurs at this time, although no information on their breeding cycles is available for these species on the Great Barrier Reef. They were found to prefer reef front situations on the Great Barrier Reef (Kiene and Hutchings, 1994a, b) which supports Rice and Macintyre's (1982) findings from the Caribbean that sipunculans occur in greatest abundance in high-energy reef crest areas, which is contrary to the findings of Bromley (1978) who found that low-energy lagoonal situations in this region were preferred. No other information is available on other factors which may determine species composition or abundances. Peyrot-Clausade and Hutchings (2002) found differences in species composition and



densities between sites, with high island sites being favored over atoll sites, but no clear relationships were seen with regards to water quality, in part due perhaps to relatively low numbers of recruits to all sites over the 5 years of the experiment. Another reason may have been that all these sites had similar depths and exposure, two factors which Rice and Macintyre (1982) suggest are important in determining distributions of this group.

Sipunculans are rarely found in coral substrates which are not covered with algae and epifauna and this is probably because boring sipunculans feed on debris and sand trapped in biota. They do not occur in the living portions of the coral colonies (Rice and Macintyre, 1982).

While most sipunculans recruit by pelagic larvae, *Aspidosiphon brocki* is known to reproduce asexually as well by constricting the posterior end to form a new individual which is then retained in the burrow (Rice, 1970).

#### *Mechanism of boring by sipunculans*

Rice and Macintyre (1972) investigated sipunculan burrows using thin sections and studied three species; and they found fine carbonate skeletal grains in the walls of most burrows examined suggesting that some mechanical abrasion has occurred during the formation of them. However, this skeletal material was not always identical to the framework in which the burrow was created, and they postulate that that it was debris associated with sponge boring on the walls of the burrow, or debris which had fallen into the burrow or internal sediment infill which was present before the sipunculan began to bore. They did find evidence of chemical dissolution as some of the coralline algal fragments and lithified internal sediment was different to the walls of some burrows. However, not all burrows exhibited these changes and they concluded that both mechanical abrasion and chemical action are involved in burrow formation. Warne (1975) concurs with this and he suggests that the variety of hooks, spines, or papillae embedded in the leathery skin of sipunculans may anchor the worm while they are boring into the substrate and perhaps aid in the mechanical grinding of acid softened substrate (Warne, 1975). Their borings are variable, most are simple, blind, straight to gently curved or sometimes highly sinuous tubes, containing a single specimen (Rice, 1969; Rice and Macintyre, 1972).

#### *Fossil data for sipunculans*

Fossil sipunculans have been recorded from the Burgess Shale, although some workers have disputed this, but no records from fossil reefs could be found.

### Sponges

#### *Diversity of sponges*

The following Orders of sponges include bioeroders, Hadromerida (Clionidae, perhaps Spirastrellidae, and the Alecionidae), the Poecilosclerida (Acanthidae, i.e., the genus *Zyzya*), the Halichondrida (Halichondriidae, i.e., the genus *Amorphinopsis*), and the Haplosclerida (Phloeodictyidae, i.e., the genus *Aka*) and there are a few “maybe eroders”

in other Orders (Hooper and van Soest, 2002; Schönberg, pers. comm.). This suggests that the ability to bioerode has developed several times within the Porifera.

The taxonomy of sponges is currently undergoing major revisions as many of the so called “cosmopolitan” species are being described as suites of new species based on molecular data, even though it is difficult to separate them morphologically (Xavier et al., in press). Ongoing revisions of bioeroding sponges indicate that they are more diverse in the Indo-Pacific (Schönberg, pers. comm.) than in the Atlantic even though the Atlantic communities are far better studied (e.g., Rosell and Uriz, 1997). A phylogenetic study of the genus *Cliona* has clearly shown that it is polyphyletic group but Rosell and Uriz (1997) preferred to maintain the genus until more detailed information was available on a wider range of taxa within this group.

#### *Succession of sponges*

While no data appears to exist on possible succession of species in coral substrates over time, there has been a widely held view that species may exhibit various growth forms with age. It has been suggested that there is an initial alpha (=papillate), later beta (=encrusting), and then a gamma-massive free living morphology (Hartman, 1958). However, Schönberg (2008) does suggest that as no single species has ever been followed from settlement to the free living form, and not all growth forms are found within a single habitat, and as most species are known only as alpha-papillate forms, it may be that different growth forms represent different species. However, Rützler (pers. comm.) disputes this and suggest that some gamma stages have been wrongly linked to certain alpha stages (e.g., *Cliona nigrescens* to *C. viridis*, in the Mediterranean). This apparent ability of some species to exhibit different growth forms could be very useful for taxonomy together with molecular data which is increasingly being used to separate species.

#### *Recruitment of sponges*

Recruitment is via pelagic larvae, but information on seasonality is not available. The clionaid sponges, one of the dominant boring groups, are found in both dead and live coral as their larvae have the ability to survive direct contact with coral polyps, but their ecological success at invading coral substrates is largely due to their ability to undermine and erode the coral skeletal base which is typically dead, thus avoiding contact with the defensive mucus and nematocysts of the coral polyp.

López-Victoria and Zea (2004) working in the Caribbean found that sponge bored fragments of coral could be redistributed across the reef and infect new coral fragments. This method of colonization can result in rapid build up of populations and may occur often after storm events.

#### *Mechanism of boring by sponges*

Detailed studies have been undertaken on the way in which sponges bore (Rützler and Rieger 1973; Pomponi,

1977, 1979a, b, and the history of sponge boring studies has been reviewed extensively by Schönberg (2008). Sponge erosion involves chemical etching of the substrate producing cup-shaped fissures and the mechanical removal of the resultant sponge chips through the sponge oscula and carried away by water currents (Neumann, 1966; Rützler and Rieger, 1973; Hatch, 1980). The etching agents are produced by specialized etching cells with filopodia which allows very localized application of the agents and enzymes. Pomponi (1977, 1979a, b) undertook detailed studies on the ultrastructure of these etching cells and she suggests that they are capable of protein synthesis, absorption, and intracellular digestion. She also found that carbonic anhydrase activity was associated with etching cell bodies, their filopodia and the spaces between them, whereas acid phosphatase activity was most intense on the outer surfaces of the cell processes but also detectable in the cell organelles. She argued that phosphatase was involved in the extra- and intracellular digestion of the organic compounds of the substrate, and carbonic anhydrase in the dissolution of the mineral components (Pomponi, 1980). Hatch (1980) was the first worker to provide the biochemical evidence to support the shifting of the carbonate equilibrium and he discusses how substrate dissolution may occur. Although Rützler and Rieger (1973) suggest that only 2–3% of the eroded substrate is chemically dissolved and the remaining removed mechanically, recent studies by Zundevich et al. (2007) suggest that far more is removed by chemical dissolution but Schönberg (2008) questions this. It may be that this ratio varies according to the group and may shift with changing environments (e.g., with ocean acidification).

Sponge boring produces characteristic traces, which are called “chambers” in the substrate which often end in minute pioneering ducts. The macroscopic patterns of chamber size and distribution have traditionally been used for taxonomic purposes (e.g., Rützler, 1974) or for measuring rates of boring (Rose and Risk, 1985). However, it has been clearly shown that a species can produce more than one kind of trace, a single trace may have been produced by several sponge species (Bromley and D’Alessandro, 1989), and these are influenced by many environmental factors, such as substrate density, water flow, and quality (Schönberg 2008). Boring also produces sponge chips which are dislodged mechanically and then transported out of the sponge galleries. These chips have characteristic shapes and morphologies which can be easily recognized in sediments, including lagoonal, inter reefal areas, concretions within previously bored substrates, etc.

Species determination can be difficult and chip dimensions have been used with some success to separate species, but sponge chip and sponge scar dimensions vary within the substrate whereas genera can be differentiated based on spicule shapes.

They tend to be larger in central established regions of the sponge boring, and with smaller diameters in pioneer regions (Rützler and Rieger, 1973). They also vary with

substrate type. Calcinai et al. (2008) working on a species of *Cliona* found that while microsculpturing of scars was similar in different substrates, other microscopic and macroscopic traces varied with substrate. They suggest this is due to the substrate microtexture.

#### *Rates of boring*

Variations in rates of boring by sponges experimentally (Bak, 1976 and references therein) suggest that rates vary according to species of sponge, substrate density (Highsmith et al., 1983; Rose and Risk, 1985; Edinger and Risk, 1997), location and depth (López-Victoria and Zea, 2005) on the reef. More material is removed from massive corals with less porous skeletons than from less massive more porous species (Buddemeier et al., 1974) and this has also been observed for the other macroborers (Hutchings, pers. observ.). Based on field observations from many geographical locations and experimental studies, other factors are also important in determining rates and abundances of boring sponges such as water flow (López-Victoria and Zea, 2005); nutrient or sewage concentration (Hutchings et al., 2005; Holmes, 2000; Holmes et al., 2000); temperature with rates in the Red Sea varying with season, and being lower in cooler areas (Mokady et al., 1993; Zundevich et al., 2007); and light especially if the sponge has symbiotic algae (López-Victoria and Zea, 2005). On impacted reefs, where many species are under stress, boring sponges thrive (Rützler, 2002; Márquez et al., 2006). Finally, rates are not constant over time with larvae or fragments freshly settling or attaching, having higher rates of growth and erosion; in contrast established colonies exhibit slow growth and low rates of erosion (Neumann, 1966; Rützler, 1975).

#### *Habitat modification by sponges*

Sponges are important in modifying habitats through bioerosion, and often physically support corals, preventing collapse after their basal structure has been eroded (Goreau and Hartman, 1963). They are also important in reef framework consolidation as they hold corals and rubble together during sediment infilling and lithification (see Wilkinson, 1983, for more details). Encrusting species of boring sponges can overgrow neighboring corals (López-Victoria and Zea, 2004; López-Victoria et al., 2006) and kill the corals.

#### *Sponges in the fossil record*

Sponges were among the first metazoans to occur in the geological records. The first reefs that were constructed primarily by sponges were in the late Ordovician period, where sponges had massive, fused, calcareous skeletons, the Stromatoporidae (Wilkinson, 1983). Kobluk and van Soest (1989) suggest that as sponges have limited preservable skeletal material, the fossil record on later reefs may be a poor representation of their importance in fossil reef systems, although the burrows would still be apparent.

## Succession of macroborer communities

Experimental studies have clearly demonstrated that a distinct succession of macroborers occurs, initially certain species of polychaetes (Hutchings and Murray, 1982) with some recruitment occurring regardless of when the substrate becomes available. A few sipunculans begin to colonize after 6 months (Davies and Hutchings, 1983; Hutchings and Peyrot-Clausade, 2002) and later on bivalve molluscs and sponges are found (Kiene and Hutchings, 1994a, b; Pari et al., 2002; Osorno et al., 2005). No studies either on the Great Barrier Reef or in French Polynesia have ever found sipunculans, molluscs, or sponges until newly available substrates have been exposed for at least 6 months, and in many cases sponges did not appear until after 4 years of exposure (Kiene and Hutchings, 1994b; Pari et al., 2002). Experimental studies have shown significant variations in recruitment patterns across a reef and within geographical areas (Kiene and Hutchings, 1994a, b; Osorno et al., 2005; Pari et al., 2002). However, these studies have usually been carried out over 2–5 years, with only one study extending for 7 and 9 years (Kiene and Hutchings, 1994a). They contrast with the “mature” communities which have well developed sponge borings, numerous large bivalves, with polychaetes restricted to large eunicids and sabellids, and these have developed over decades, rather than the few years over which experimental studies have been conducted. It is these “mature” communities which have been typically described in the literature (Neumann, 1966; Hein and Risk, 1975; Hudson, 1977; MacGeachy, 1977; Risk and MacGeachy, 1987; Davies 1983).

All these macroborers which have characteristic shaped burrows must maintain an opening to the outside to obtain a continual supply of fresh oxygenated water, food supply and for the release of excretory and reproductive products, but they cannot leave the substrate as they are effectively entombed within it. Examination of many cut surfaces clearly shows that burrows of different organisms rarely if ever touch or coalesce and presumably boring creates vibrations to which other borers are sensitive and allows them to take the necessary avoiding action.

## Grazers

### Echinoids

In the Indo-Pacific the main grazing species belong to the following genera, *Diadema* (Figure 1f), *Stomopneustes*, *Echinothrix*, *Echinostrephus* (Figure 1g), and *Echinometra*, with *D. savigny* and *Echinometra mathaei* (Figure 1d) often being the two most conspicuous species. In the Caribbean, the two most common species are *Diadema antillarum* and *Echinometra viridis*, so while these genera are also present in the Indo-Pacific, different species are present.

### Method of grazing

Echinoids use their Aristotle's lantern specialized plates of the mouth (Figure 1e) to grind the coral substrate into a paste which is then swallowed and the contents of the

ruptured algal cells are then absorbed by the gut. Such grazing occurs mainly at night with the echinoids leaving their crevices and roaming over the reef and fresh feeding scars can be seen in the morning (Figure 1g). Faecal pellets produced, consist almost entirely of ground up calcium carbonate and these are deposited on the substrate or on the lagoon floor.

### Rates of grazing

Rates of bioerosion by *E. mathaei* have been estimated at  $6.9 \pm 2.2 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$  in French Polynesia at Faavaa, Tahiti, a very degraded reef where overfishing has occurred, lower rates were found at nearby Moorea of  $4.3 \pm 3.6 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$  (Figure 4). Rates of  $8.3 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$  were estimated for the reef flat at Reunion, Indian Ocean (Peyrot-Clausade et al., 2000) and similar rates were recorded at Diani reef in Kenya (McClanahan and Muthiga, 1988), both of these reefs have also been subjected to overfishing. In the Caribbean on degraded reefs, rates of grazing by echinoids can exceed  $22 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$  (Glynn, 1988; Reaka-Kudla et al., 1996) where the dominant species is *Eucidaris thouarsii*. On the Great Barrier Reef, Australia, densities of grazing echinoids are very low (Sammarco, 1985) and this may be in part due to healthy fish populations which predate on juvenile echinoids. While echinoids have typically been regarded as grazers feeding on endolithic algae, some species of the family Echinometridae are active borers especially in high energy situations (Asgaard and Bromley, 2008). For example, *Echinometra lucunte* which occurs in the Caribbean and the Atlantic produces cup-shaped burrows as juveniles and it is suggested that these burrows enable the echinoid to catch drift algae with their spines, as well as grazing on the turf and endolithic algae on the walls of the burrow. Adults tend to occupy elongated grooves and presumably both types of burrows provide shelter from wave action and the species tends to stay within the confines of their burrow. A similar behaviour is exhibited by *Echinometra mathaei* in the Western Pacific especially in the high-energy environments outside barrier reefs, although they do leave their burrow at night especially in a lagoonal situation (Peyrot-Clausade et al., 2000). Details about the other echinometrid echinoids are given by Asgaard and Bromley (2008) together with some excellent illustrations of the various species and their burrows and they summarize all the information that is available on each species and provide rates of grazing where known.

### Echinoids in the fossil record

Similar genera of grazing echinoids have been recorded from fossil reefs although as Greenstein (1993) explains they are not well conserved as their fragile skeletons do not preserve well so that abundances may be severely underestimated.

### Molluscs

A high diversity of gastropods and a lower diversity of chitons occur on reefs, with distinct faunas in the Indo-Pacific and Atlantic.



### Method of grazing

Gastropod molluscs and chitons can be responsible for considerable losses of substrate on intertidal reefs. They use their radulae to remove the surface layers and the embedded endolithic algae and like the parrotfishes and echinoids they are able to break down the algal walls and utilize the contents of the plant cells. Chitons excavate a home scar to which they return to, after foraging, mainly at night during low tide. They may be locally abundant on intertidal reef flats.

### Rates of grazing

A recent study at One Tree Island, Great Barrier Reef based on *Acanthopleura gemmata*, estimated rates of erosion of 0.013–0.25 kg CaCO<sub>3</sub> m<sup>-2</sup> year<sup>-1</sup> at two sites on the reef margin and on the beachrock platform (Barbosa et al., 2008) (Figure 2a). While these figures are much lower than those for echinoids and scarids they can be very important in some habitats.

### Grazing on live corals

The gastropod *Drupella* feeds on live coral (Shafir et al., 2008; Lam et al., 2007) as does the Crown of Thorns Starfish (*Acanthaster planci*) (DeVantier and Done, 2007 and references therein) and the resultant dead coral then becomes available for colonization by borers. Gastropods belonging to the genus *Duprella* are obligate corallivores and specialize on acroporid coral especially *Acropora* and *Montipora* spp. (Morton et al., 2002). Recently large colonies of *Platygyra acuta* and *Platygyra carnosus* were observed in Hong Kong to be severely eroded at their bases which makes them very susceptible to storm damage. This erosion was caused by the gastropod *Drupella rugosa* which was feeding on the living coral tissue and then by grazing of the newly available substrate which had been colonized by endolithic algae by the echinoid *Diadema setosum* (Lam et al., 2007). A recent review by Morton and Blackmore (2009) suggests that the dense concentrations of *Drupella rugosa* and another corallivorous gastropod *Cronia margaritcola* regularly seen in Hong Kong Harbour are not plagues but rather breeding aggregations and they actually doubt that these gastropods pose a threat to the corals, contrary to the findings of Lam et al. (2007). However, there are well-documented cases in which localized population outbreaks of *Drupella* spp., as well as the starfish, *Acanthaster planci* and can rapidly and severely reduce the percentage cover of live coral, although some reefs subsequently recover (Glynn, 1973; Colgan, 1987).

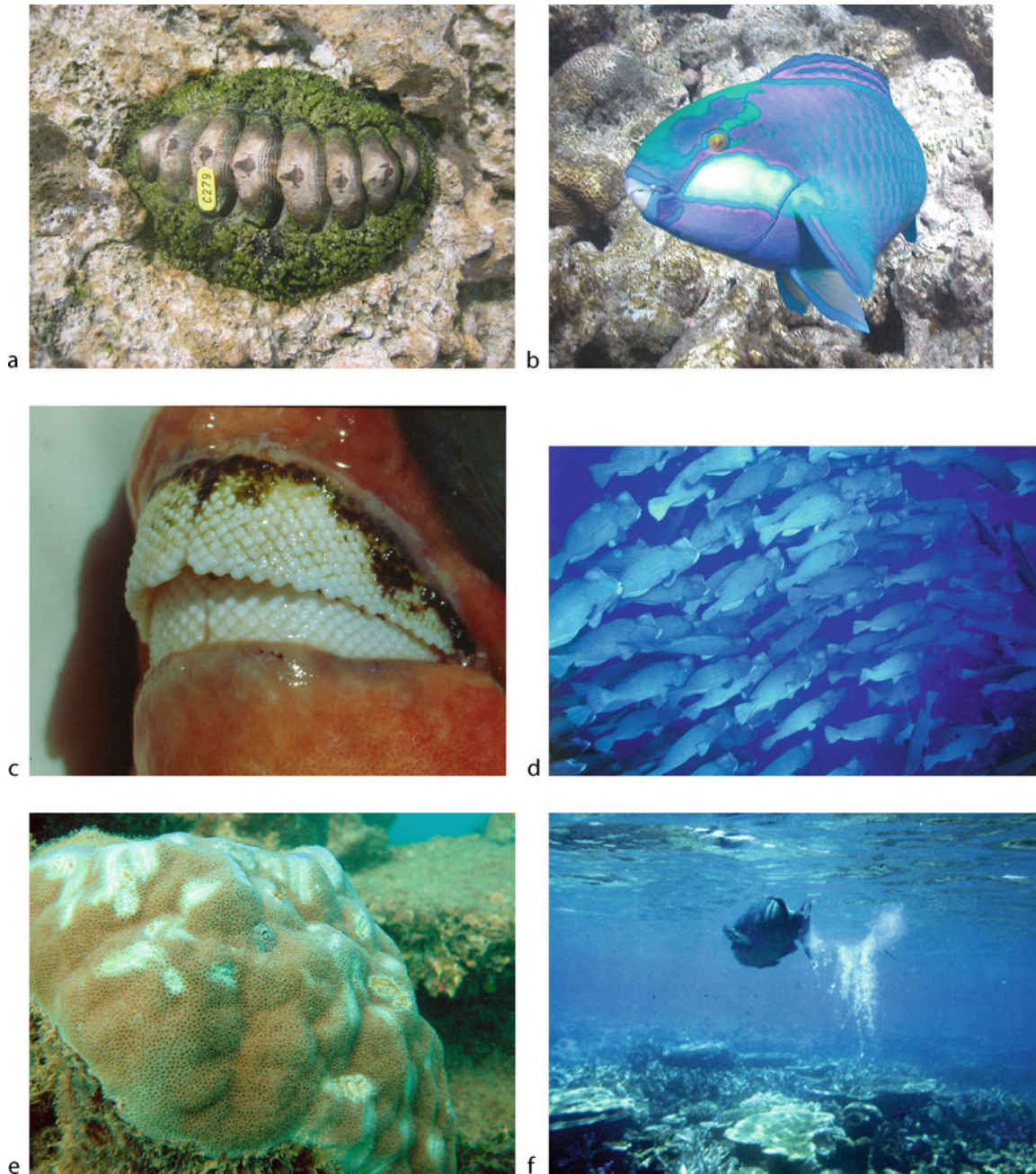
### Parrotfishes

The Scaridae, a family of labroid fish, are highly characteristic of coral reef habitats. With few exceptions their geographical distribution is linked to tropical reef environments. Compared to other tropical perciform fish, their diversity on the reef is not that great, with about 25 described from the Great Barrier Reef (Choat and Randal, 1986). While some of these have Indo-Pacific distributions others have

restricted ranges. In the Caribbean, 15 species are present, and those in the genera *Cryptotomus*, *Nicholsina*, and *Sparisoma* are restricted to this area. The genus *Scarus* is the dominant Indo-Pacific genus and there are six species in the Caribbean that appear to be fairly recent colonizers; *Sparisoma* has been there for much of the Tertiary. Only one Caribbean parrot fish *S. viride* has the capacity to significantly bioerode calcareous substrata compared to several species in the Indo-Pacific (*Bolbometopon muricatum*, *Cetoscarus bicolor*, and the five large species of *Chlorurus*). Additional species occur off the African coast and of Brazil (Choat, pers.comm.).

### Method of grazing

It is the presence of dense colonies of endolithic algae which attracts numerous grazing scarids or parrot fish to both live and dead coral (Figure 2b). Scarids or parrotfish, now regarded as belonging to the Labridae family (Cowman et al., 2009); can be divided based on jaw morphology into excavators which remove pieces of the substrate (Figure 2b) and scrapers (Figure 2e) which have a nonexcavating bite just removing material from the surface of the substrate. Schools of parrotfishes can often be seen and heard feeding in the late afternoon in shallow waters (Figure 2d) and distinctive grazing marks are visible on the surface of both live and dead coral substrates (Figure 2e). While most parrotfishes feed on dead coral substrates the large *Bolbometopon muricatum* has a diet which consists of over 50% of live corals (primarily *Acropora* species, Bellwood, 1986) (Figure 2c). Some others that graze on *Porites* spp., occasionally, include the excavators *Scarus gibbus* and *Cetoscarus bicolor* and the scrapers *Scarus frenatus* and *S. rivulatus* on the Great Barrier Reef, Australia. Such findings are contrary to the traditional view that parrotfishes feed on dead coral substrates and recent studies in the Caribbean have shown that feeding on live coral can also be widespread. A study on the back reef habitat at Carrie Bow Cay, Belize in the Caribbean, found that parrotfish predation on the reef building coral *Porites astreoides* was significant with >13% of colonies exhibiting partial or total colony mortality (Rotjan and Lewis, 2005). A suite of parrotfishes were present but probably the most important species was *Sparisoma viride*. Not only were the fishes targeting the endolithic algae but in grazed areas of the colonies there were significantly higher densities of macroborers namely barnacles, polychaetes, and vermetids. Rotjan and Lewis (2005) speculate that the parrotfishes were targeting such areas to obtain additional nutritional benefits from these macroborers. Subsequent studies by Rotjan and Lewis (2006) investigated the spatial and temporal patterns of parrotfishes across habitats on the Belize barrier reef. They found that parrotfishes were selective in the live corals on which they grazed. The most heavily targeted species were all members of the *Montastrea annularis* species complex, and colonies of *M. cavernosa*, *Agaricia agaricites*, *Diploria strigosa*, *Porites astreoides*, and *Porites porites* were not heavily targeted. Parrotfishes also



**Bioerosion, Figure 2** (a) Close-up of *Acanthopleura gemmata* from One Tree I., nestled onto its home scar (photo: B. Kelaher). (b) The parrot fish *Scarus* sp. with well developed jaws about to take a lump of dead coral substratum full of endolithic algae (photo: O. Hoegh-Guldberg). (c) Jaws of *Bolbometopon muricatum* on the outer barrier near Lizard I. (photo: D. Bellwood). (d) Schools of *Bolbometopon muricatum* at Osprey Reef, Coral Sea (photo: P. Hutchings). (e) Bite marks of a scarid and a boring barnacle embedded in *Porites lutea* (photo: O. Hoegh-Guldberg). (f) Defaecation by parrotfish, fine sediment produced by the grinding of the ingested coral fragments (photo: D. Bellwood).

exhibited differences in preferred coral species depending upon habitat, with *M. annularis* being preferred in shallow habitats, whereas *M. franksi* was consumed more at depth and *Siderastrea siderea* was preferentially grazed only in the spur and groove habitats. Given that numbers of

*Sparisoma viride* and *Sp. aurofrenatum* increased between 1982 and 2004 on the Belize barrier reef, there would have also been a corresponding increase in grazing on live coral and the impacts of this on coral survival needs to be evaluated (Rotjan and Lewis, 2006).



Once excavating species have bitten off fragments of substrate, the fragments pass into the muscular pharyngeal mill at the beginning of the gut. The mill consists of grinding surfaces covered in teeth which are continuously replaced, and as these surfaces are moved back and forwards the coral fragments are broken down into a fine powder releasing the algae and breaking the plant cells releasing the nutrients which are then absorbed by the fish and the fine powder is released into the water column (Bellwood and Choat, 1990) (Figure 2f). It has been shown that the gut contains the necessary enzymes to breakdown the cellulose plant walls (Choat et al., 2002).

#### *Rates of grazing*

Rates of grazing by parrotfishes (Figure 2e) have been estimated from 0.61 to 1.68 kg CaCO<sub>3</sub> m<sup>-2</sup> year<sup>-1</sup> in Barbados (Frydyl and Stearn, 1978), 0.05 to 0.9 kg CaCO<sub>3</sub> m<sup>-2</sup> year<sup>-1</sup> at La Réunion, Indian Ocean to 0.7–3.30 CaCO<sub>3</sub> m<sup>-2</sup> year<sup>-1</sup> at Moorea, French Polynesia (Peyrot-Clausade et al., 2000), 0.9–3.89 kg CaCO<sub>3</sub> m<sup>-2</sup> year<sup>-1</sup> – on inner reefs, increasing to 5.2–8.4 kg CaCO<sub>3</sub> m<sup>-2</sup> year<sup>-1</sup> on mid shelf reefs and 32.3 kg CaCO<sub>3</sub> m<sup>-2</sup> year<sup>-1</sup> on the outer shelf reef crest and 23.1 kg CaCO<sub>3</sub> m<sup>-2</sup> year<sup>-1</sup> on the reef flat with very little erosion occurring on the outer shelf reef slope or back reef habitats (0.8–1.8 kg CaCO<sub>3</sub> m<sup>-2</sup> year<sup>-1</sup>) on the Great Barrier Reef (Hoey and Bellwood, 2008). In part this is a reflection of the distribution of grazers across the reef (Russ, 1984) which has been well documented for the Great Barrier Reef. A variety of methods have been used to estimate these rates so that some caution needs to be taken in interpreting these results and obviously rates depend on species, size of individuals, location of study both within and between reefs and methods used. Some workers have measured the amounts of calcium carbonate in the gut (Peyrot-Clausade et al., 2000) whereas others (Bellwood, 1986; Bruggemann et al., 1996; Frydyl and Stearn, 1978; Rotjan and Lewis, 2005, 2006) have measured the size of the bite marks, depth of excavation and observed the frequency of feeding and calculated the amount of substrate removed and factored in size and densities of the fish populations to obtain rates of loss over the reef.

On healthy reefs, bioerosion by parrotfishes is the dominant agent of grazing, and typically loss of substrate by these fishes across the reef tends to be balanced by net calcification (Hoey and Bellwood, 2008).

#### *Evidence of grazing from fossil reefs*

Parrotfishes are well preserved on fossil reefs and the oldest ones including a species of *Bolbometopon*, an eroder are all of Miocene age (Bellwood and Schultz, 1991). Molecular data suggest that the basal parrotfish division into seagrass and reef clades occurred approximately 42 million years ago (Streelman et al., 2002). Although the feeding mode of the reef clade is equivocal, the origin of this lineage at 42 Ma provides an independent estimate of the maximum age of parrotfish bioerosion. The impact of herbivores, therefore, may have had two phases, with a rise in nonexcavating grazing prior to the early

Eocene and the advent of deep excavating fish herbivory sometime later, between 42 and 5 Ma (Bellwood, 2003). Obviously interactions between herbivory and coral reefs have been occurring for a very long time with changes in the composition of the coralline algal crusts of substrates associated with an increase in the density of fish grazers (Bellwood, 2003, Figure 7). Much of this evidence is from analyzing the mouth parts of the fish present in various fossil reefs, as actual bite marks or evidence of grazing are unlikely to have been preserved. More recent molecular studies are confirming these timelines (Read et al., 2006).

#### **Predation on live coral**

A great variety of organisms prey on live coral predators and Rotjan and Lewis (2008) provides a detail list by species (includes both vertebrates and invertebrates) and geographical regions. They distinguish between species which remove only mucus, coral tissue, or skeleton, and they provide rates of consumption reported in the literature, which were based either on the number of bites per minute or the % of live coral in the gut.

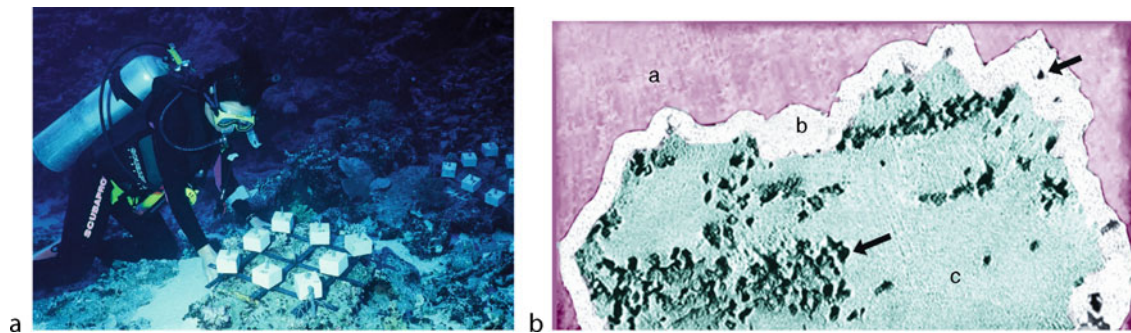
All this grazing activity which removes the surface layer of the coral substrate exposes a new surface which is then rapidly recolonized again. Grazers while targeting the endolithic algae also collect any other type of boring organisms living in the surface layers of the coral skeleton (Rotjan and Lewis, 2005).

#### **Determining rates of bioerosion**

Experimental studies have measured rates of bioerosion using blocks of recently killed colonies of *Porites* which have been attached to the substrate for varying lengths of time (Figure 3a). Blocks are then sliced and measured and changes in dimensions determined, to determine loss of substrate by external grazing, increases in dimensions by accretion of coralline algae and losses by internal erosion by macro and microborers (Figure 3b). Rates of loss by borers involve calculating the volume of the burrows and because of their characteristic shapes and sizes they can be apportioned to each of the major groups of borers. By knowing the density of the coral substrate the amount of calcium carbonate lost can be calculated and then figures extrapolated to amounts per m<sup>-2</sup> year<sup>-1</sup> although obviously the distribution of substrate available for colonization is not uniform across a reef. These rates also include loss of substrate by physical and chemical erosion but separating them from losses caused by bioerosion is almost impossible (Peyrot-Clausade et al., 1995). All these processes also act synergistically, for example as the substrate becomes honeycombed by borers this facilitates physical erosion as water is flushed through the substrate, or when pieces of substrate are removed by grazers, new surfaces are exposed facilitating further losses by chemical and physical erosion.

Rates of loss will vary across the reef depending on the amount of live coral cover present as well as the morphological types present (massive, plate, branching, encrusting) and the amount of dead coral substrate of varying ages





**Bioerosion, Figure 3** (a) Experimental study of bioerosion at Osprey Reef, Coral Sea, two replicate grids with newly laid coral blocks to be exposed for varying lengths of time (photo: J. Johnson). (b) Diagrammatic representation of coral block illustrating how the various components of bioerosion (i.e. grazing, accretion and boring) are determined from a series of sections through each block. Knowing the density of the coral block, these measurements can then be scaled up to rates per square metre and then net rates of bioerosion calculated. a, original block; b, accretion; c, block remaining after grazing and boring.

(i.e., time since death of coral colony) present, as rates tend to increase with increasing maturity of boring communities (Peyrot et al., 1992). While most studies on the distribution of boring communities have focused on the massive coral *Porites*, all corals are bored once they die, but dense coral skeletons are most impacted. Comparing rates of bioerosion across or between reefs must be carefully considered as rates vary according to amounts and types of substrate available. Rates will also vary over time as the composition of boring communities change and may stabilize as the component individuals mature. Rates of grazing and accretion may vary over time and sediment may also be washed into the burrows created by the borers, recemented and thus strengthening the substrate, so just comparing rates of bioerosion can be fairly meaningless unless information on all the components contributing to the balance between reef growth and destruction are known.

In addition to calculating rates of loss by internal erosion, it is important to identify the organisms responsible for these losses. The easiest method for extracting the macroborers is to dissolve the substrate in a weak acid solution and sort the residue into the relevant groups and identify to species. However, typically the volume of the macroborers is lower than the loss of substrate calculated from measuring the size of the burrows and this probably is a reflection that some of the borers have established themselves in the substrate and then died during the exposure period but their burrows remain (Pari et al., 2002). Determination of the species composition of the microborers requires a variety of techniques, see Tribollet (2008). Amongst both the micro and macro- borers there appears to be some widely distributed species, however it may be that with more detailed taxonomic investigations involving both morphological and molecular techniques that suites of cryptic species will be found.

Another method of calculating rates of bioerosion is to collect large heads of dead coral of known age, slice them and measure the loss of substrate by internal erosion and extrapolate to losses per  $\text{kg m}^{-2} \text{ year}^{-1}$  (Hudson, 1977). This makes the assumption that rates of boring are

consistent over time but we know that this is not correct and so such methods of estimating rates may be of limited value. Examining such heads of dead coral often reveals that much of the erosion occurs at the base of the colony and this may make the colony more susceptible to being dislodged during storms or when large heads of corals are rolled down the reef slope during a storm clearing everything in its path. Although there are some data to suggest that heavily sponge bored coral heads may be more flexible and able to withstand some storm activity, other data from branching corals indicate the reverse that such colonies are more susceptible to being damaged (López-Victoria and Zea, 2004; Chaves-Fonnegra and Zea, 2007).

### Habitat creators

Bioerosion, as well as generating sediment, which may either be washed out of the substrate and contribute to inter reefal and lagoonal sediments or retained within the burrows and subsequently become cemented, also creates a 3D habitat. The creation of this habitat provides suitable refuges for a wide variety of invertebrates and some of the smaller fish species and is referred to as the cryptofauna or nestlers. This is where the majority of reefal biodiversity and productivity resides and is a critical component of reefal food chains, trapping sediments, and recycling mucus, providing food for many other organisms. While much of the cryptofauna lives permanently within the substrate, some venture out at night to feed or extend their tentacles, arms or feeding crowns, etc., out over the surface of substrate to feed. This fauna cannot themselves bore but they occupy the vacant burrows created by the borers. Some cryptofauna are preyed upon by a range of other organisms, for example, species of the gastropod *Conus* feed selectively on certain species of polychaetes. *Conus* uses its proboscis to suck out these species from within the coral substrate (Kohn and Nybakken, 1975) and some species are highly selective as to which species of polychaetes they prey upon. One presumes that within the substrate the borers and cryptofauna function as an ecosystem

with animals preying upon each other, feeding on the endolithic algae and recycling sediment and mucous trapped within the substrate. A few studies have attempted to quantify the density and diversity of this combined community (Grassle, 1973; Kohn and White, 1977) which is very diverse and abundant although the taxonomy of many of the groups is poorly known. As well as errant species of cryptofauna there are many encrusting species of bryozoans, sponges, and ascidians which utilize these burrows all contributing to the incredible diversity of coral reef invertebrates.

### Environmental factors influencing rates and agents of bioerosion

Studies have shown that rates and agents of bioerosion exhibit spatial and temporal differences (Kiene and Hutchings, 1994b) within a single reefal system, subtidal reef slopes, and lagoonal sites experienced higher rates of grazing than deeper sites and reef flats and these differences were maintained in experimental substrates exposed for 9 years (Kiene and Hutchings, 1994a). These differences could be explained by the distribution of the dominant parrotfish in the region. Many of the boring organism exhibit seasonal variation in recruitment and these patterns are influenced by prevailing winds (Hutchings and Murray, 1982) but storms may modify these patterns transporting larvae to unsuitable habitats.

Experimental studies have also shown that the composition of both the micro and macroboring communities varies not only according to site but to environmental conditions (Hutchings et al., 2005). Inshore sites with heavy sedimentation from river run off are characterized by deposit feeding polychaetes and filter feeding sponges and low densities of endolithic algae are restricted due to light availability which reduced levels of grazing. In contrast communities further offshore in clear waters with little or no sedimentation are characterized by high rates of bioerosion due to grazing and internal bioerosion by macroborers such as bivalves and filter and surface deposit feeding polychaetes (Osorno et al., 2005; Hutchings et al., 2005).

Reefs have always been subjected to storm events and probably plague events such as Crown of Thorns starfish, which leads to a temporary increase in dead coral substrate and local increases in rates of bioerosion, over time these reefs recover providing surrounding reefs are “healthy” (Brodie et al., 2005) and the balance between reef growth and reef destruction is restored. But increasingly this balance is being changed with losses exceeding gains and the next section discusses the factors which are disrupting this balance.

### Anthropogenic factors influencing rates and agents of bioerosion

#### Poor water quality

Experimental studies have shown that rates of microbioerosion and erosion by grazing predominantly

by parrotfishes increased when nutrients are added to the water column (Osorno, 2005). Studies in French Polynesia at selected sites which were subjected to both increased sediment loads and elevated nutrients and significant differences were found between sites some of which were separated by thousands of kilometers. Both eutrophic and pristine sites exhibited high rates of bioerosion although the processes responsible for this loss differed. At the most eutrophic site Faaa, Tahiti, rates of loss were largely due to grazing by echinoids especially *Echinometra mathaei*, whereas at the pristine site at Tikehau, high rates of internal bioerosion were due to sponges (Pari et al., 2002). At Faaa, densities of  $201 \pm 60.4$  indi  $m^{-2}$  of echinoids were recorded (Pari et al., 1998) and an almost complete absence of herbivorous fish especially parrotfishes, due to overfishing. A river flowing out on this lagoonal site at Faaa is highly polluted as untreated sewage and other organic pollutants are allowed to be discharged into this river. These eutrophic conditions allow dense populations of free standing algae and endolithic algae to flourish and which are heavily grazed by the echinoids (Figure 4). This grazing activity together with dense algal cover severely limits the successful recruitment of coral larvae and at this site the balance between reef growth and reef destruction is strongly skewed toward reef destruction. Pari et al. (2002) estimated a loss of reef framework of  $6.87 \pm 2.16$  kg  $m^{-2}$  year $^{-1}$  at this site (Figure 4).

Field studies in the Grand Caymans found a marked increase in the biomass of the boring sponge *Cliona delitrix* in the coral *Montastrea cavernosa* in areas on the fringing reef affected by the discharge of untreated sewage. This resulted in a significant loss of coral skeleton which was reduced to silt-sized sediment and so the proliferation of a bioeroding organism in the sewage-stressed environment has caused a shift in the carbonate balance on the reef (Rose and Risk, 1985). Similar results were found in Indonesia with polluted sites exhibiting higher rates of bioerosion both of live massive corals and



**Bioerosion, Figure 4** Experimental blocks after six months showing extensive grazing by *Echinometra mathaei* at Faaa, Tahiti (photo: M. Peyrot-Clausade).

branching coral rubble compared to relatively unpolluted sites (Holmes et al., 2000).

Studies in the polluted Hong Kong Harbour showed that stressed corals were more extensively bored than healthy ones (Dudgeon and Morton, 1982) and weakened the skeleton making it more susceptible to storm damage. In contrast low densities of mollusc borers in healthy corals may actually strengthen the substrate as *Lithophaga* lines its burrows with aragonitic secretion (Barthel, 1982).

Both experimental and field studies show that while eutrophic sites experience high levels of bioerosion (Reaka-Kudla et al., 1996; Cortes, 1993; Holmes et al., 2000), pristine sites may also exhibit elevated rates (Pari et al., 2002). So high rates per se do not always indicate poor water quality.

### Increasing water temperatures

Sites in the Caribbean with extensive stands of the elkhorn coral *Acropora palmate*, which were subjected to massive mortalities and bleaching during the 1980s, now consist of broken dead stands covered by the encrusting and excavating sponge *Cliona tenuis*. As the sponge undermines the branches of coral, they break off and during storms they are thrown against new coral hosts and the sponge is able to colonize a new uninfected coral colony. The times of initial colonization of the corals by the sponges was related to the timing of hurricanes in the area. In addition to infecting the dead branches, the sponge was also undermining encrusting and foliose corals settling on the dead *A. palmata*, retarding the recovery of these reefs (López-Victoria and Zea, 2004).

Extensive mortality of corals from bleaching at Uva Island, Panama caused by the prolonged 1982–1983 El Niño event, led to significant increases in echinoid grazers and increased rates of internal bioerosion led to significant loss of reef framework and collapse of reef walls (Eakin, 1992).

Kleeman (2008) working on reefs in the Maldives after a severe bleaching event found dense concentration of the bivalve *Parapholas quadrizonata* with boreholes reaching 80 mm in length and 25 mm in diameter and he estimated life spans of 3–8 years probably 10 years. Thus a continual supply of larvae is being produced and as many of the reefs have less than 50% live coral cover following the severe bleaching event in 1998, this has resulted in an accelerated rate of loss of reefal substrate as suitable dead coral substrate is available for colonization by the bivalves (Kleeman, 2008).

### Cumulative impacts

Initially many of these anthropogenic impacts were related to the location of most coral reefs in developing countries with increasing urbanization and declining water quality in part due to lack of sewage treatment works, unregulated coastal development leading to excessive land run off, loss of riparian vegetation along the rivers flowing onto the reefs, overfishing and inappropriate fishing techniques

such as dynamite fishing and collecting of coral for building and inappropriate dredging in lagoons. Typically, this has led to damaged fringing reefs close to centres of population. These same communities were also exploiting the reefs as tourist attractions earning valuable revenue with often the nearby hotel developments also impacting on these reefs. But during the 1980s increasing records of widespread bleaching of coral were being recorded, while some bleached coral colonies recovered many did not. Satellite imaging of surface water temperatures allowed the areas where bleaching was likely to occur to be determined and subsequent surveys often supported these predictions. As well as the duration of elevated water temperatures other factors such as water quality seemed to be involved in determining the recovery of the reef as well as location of nearby unaffected reefs. Increased incidences of bleaching around the world highlighted the impact of climate change on reefs, and it became evident that reefal ecosystems are one of the most vulnerable to climate change. A recent vulnerability assessment of the climate change on the Great Barrier Reef (Johnson and Marshall, 2007) is a sobering analysis of the various aspects of reefs, which are changing, not just elevated temperatures, increased storm intensities, increased run off, increasing alkalinity, rising sea levels, and changes in oceanography which will impact on recruitment processes, increased disease and invasive species, for example. Many of these impacts will result in increased amounts of dead coral substrate and thus higher rates of bioerosion of reef framework (Hutchings et al., 2007; Przeslawski et al., 2008). Loss of reef framework will impact directly on those organisms which either feed or live on live coral, change fish communities (Cinner et al., 2009) which will have serious economic consequences for many people. Tourism revenues will decline and low lying areas which are currently protected from storms will lose this protection and low lying areas will become inundated as sea levels rise. Many of the coastal settlements lack the financial resources to protect these areas and we are already seeing that people are being relocated from such areas.

### Conclusions

While over the past 20 years or so, our understanding of the processes of bioerosion has increased considerably, many gaps remain, especially as to the mechanisms of boring and the interactions between borers and grazers. Our knowledge is best for the Caribbean, Great Barrier Reef, and French Polynesia, with little information available from the Western Indian Ocean, Red Sea, and SE Asia. There is an urgent need to continue studies on the impact which water quality and sediment loads have on rates and agents of bioerosion and how these will change with increasing ocean acidification and rises in seawater temperatures.

As reefs are increasingly being subjected to anthropogenic impacts many of which act synergistically, it is becoming critical to develop monitoring techniques which



could provide an early warning system that a particular reef is under stress and subject to increased rates of bioerosion. In some cases, an increase in densities of echinoids may be sufficient to alert the managers that significant overfishing is occurring, water quality is declining or turbidity is increasing, so that remedial action can take place. An alternative may be to develop methods of quickly assessing the level of sponge colonization of coral rubble as a level of eutrophic conditions. Existing data clearly show that after a massive mortality of corals from a bleaching event, Crown of Thorns plague etc., levels of bioerosion significantly increase and those reefs that do recover are those where water quality is good, turbidity levels are low, and fish populations are healthy, and there are nearby "healthy" reefs that can act as source reefs to re-establish the coral communities. In contrast if these conditions are not met then substantial loss of reef framework occurs and the balance between reef growth and reef destruction is not restored, leading to loss of biodiversity and considerable economic and social consequences of the loss of coral reefs.

## Acknowledgments

The author would like to thank the following for providing references and comments on various drafts of this manuscript, Christine Schönberg, David Bellwood, Winston Ponder, Klaus Rützler, Ian Macintyre and Howard Choat and to David Hopley for the invitation to contribute to this book.

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## Cross-references

Algae, Blue-Green Boring  
Carbonate Budgets and Reef Framework Accumulation  
Microbes  
Nutrient Pollution/Eutrophication  
Reefal Microbial Crusts  
Solution Processes/Reef Erosion

## BIOHERMS AND BIOSTROMES

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## Definitions and history

The words were coined by Cumings (1932), a *bioherm* being defined as a *mound or lens-shaped organic build-up, edited by the skeletons of various organisms and lying unconformably inside a stratigraphic series of different lithology*. Conversely, a *biostrome* is a *flat layered reef structure, wide or narrow in shape and causing no stratigraphic disturbance inside its sedimentary environment*. In this original meaning both formations were conceived as *stratigraphic units* and neither the biotic conditions for their development nor steric disposition of their elements were taken into account.

- For the Encyclopaedia Britannica a bioherm is defined as “an ancient organic reef of moundlike form built by a variety of marine invertebrates (and coralline algae). A structure built by similar organisms that is bedded but not moundlike is called a biostrome.”

- For Battistini et al. (1975) a bioherm is a: “lens-shaped organic reef... embedded in situ inside sedimentary layers of different lithological nature... it may be surrounded by a peripheral talus of biodetrital sediments,” whereas a biostrome is a “layered, bank like organic reef of variable extension, creating no discontinuity inside the embedding sedimentary layers.”
- Kershaw (1994) introduces a number of complementary terms: the constructing organisms may be mostly in situ (*autobiostromes*), or mostly as debris included in the structure (*parabiostromes*), with *autoparabiostrome* as intermediate. Conversely, *allobiostromes* are formed of material derived from allochthonous sources, for example skeletal plankton sedimented onto the sea bed.

## Discussion

Although these terms may be useful, there is no general agreement on a complete definition taking into account *at one and the same time* such different characteristics as age, stratigraphic conformity or unconformity, along with the autochthonous or allochthonous nature of deposited organisms. As a consequence, many biologists and geographers use “bioherm” as a general term not only for major biological build-ups such as algal rims or coral reefs (e.g., see Adey and Burke, 1976) but also for small-scale organic build-ups, for which the word “biostrome” would suit better.

Further difficulties come from the fact that relationships with embedding layers are not visible on living formations. For example, an algal rim growing on the outer edge of a coral reef is indeed a bioherm, or a part of it since it takes an active part in the edification and protection of the latter, but a thin algal layer coating a limestone or volcanic shore, or lining a vertical cliff without altering local sedimentation should be called a biostrome even if both formations are in continuity with one another.

Furthermore, actualists consider detrital accumulations of dead shells and broken skeletal material (generally mud-supported and harboring a completely different infauna) as quite different from true build-ups or reefs which are in situ developed formations.

For these reasons bioherm and biostrome cannot be put into automatic correspondence with the highly diversified terms used by actualist reef geologists or biologists, since additional factors such as size of the buildup, thickness, relation with the sea-surface, and resistance to waves must be taken into account. Chronology is also important: most reef complexes are vertical successions of layers corresponding to successive glacial low and high sea-levels.

Initially there was no size limitation in the definition of bioherms and biostromes, and they vary from microbioherms formed by a single colony to coral knolls of decametric size. Nevertheless a general agreement exists to limit the use of the latter words to structures important enough to be easily positioned and mapped.

This, in turn, creates a problem since minor built structures such as algal rims or coral knolls may be of metric or decametric size and difficult to cartography. *In fact, bioherms and biostromes are part of a same continuum.*

Ecological factors are also important.

- *Bioherms*: mainly develop in favorable ecological conditions, growth is three-dimensional, and biodiversity high to oligospecific. Sediment accumulation and diagenesis may be high, leading to *bafflestone*, *framestone*, or *boundstrome* structures (*sensu* Bathurst 1971). Bioherms growing near the surface may lead to true wave-resistant reefs but deep-water coral formations may be called bioherms but certainly not reefs. In the same manner the thick calcareous algal build-ups developing below –30 m (“coralligene”) in the Mediterranean might be called bioherms since, although relatively thin (a few meters thick), they alter both bottom profile and sedimentation (Laborel 1961)
- *Biostromes*: often develop in adverse ecological conditions and their importance depends on such factors as depth, exposure and hydrodynamics, temperature, and sedimentation. They tend to be oligo or monospecific. Algal rims and ridges are linked to strong exposure to surf, as well as pavements of calcareous algae covering the bottoms of reef passes with strong tidal currents. Corals may also develop biostrome-like, for example sheet-like patches of *Siderastrea* along West African and Cape Verde Islands rocky coasts (Laborel, 1974), or western tropical Atlantic *Montastrea cavernosa* developing monospecific layers down to –60 m.

For the geologist, biostromes and bioherms are *fossil* formations - meaning that after their living phase they were killed, eroded, or reworked and covered by younger sediments. Their detail morphology is therefore altered - erosion and sedimentation tending to erode reliefs and fill lower points. This has an over-simplifying effect when using fossil coral-reefs as sea-level markers. Blanchon and Blakeway (2003) recently called attention to such difficulties.

## Conclusions

Unless bio-accumulated detrital mounds and layers are taken out of the definition of bioherms and biostromes and given a different name (a decision that only geologists can take), and the status of small-scale build-ups is settled, *use of the words bioherm and biostrome should preferably be restricted to the fossil formations for which they were coined* (whether their associated detrital facies, and other types of detrital formations are included or not). Students of living reefs are hence encouraged to prefer more general terms (such as “biological build-up,” “reef-like structure,” or “biogenic construction”) instead.

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## Cross-references

[Algal Rims](#)  
[Coral Reef, Definition](#)  
[Sea-level Indicators](#)

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## BIOTURBATION

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### Definition and introduction

Bioturbation refers to particle mixing within unconsolidated sediments through the activities of biological organisms, most commonly at, or close to, the water-sediment interface. The implications of this process go far beyond simply mixing the substrate as sediment particle preservation, food availability, and geochemical composition within the substrate are all affected. Bioturbation activity can also increase the size of the effective sediment-water interface contributing to enhanced chemical fluxes between the sediment and the water column. Some organisms enhance chemical exchange by flushing their burrows with the overlying waters, a process termed bioirrigation (Aller, 1977). Others, mainly macroinfauna (e.g., annelid worms – polychaetes), feed at depth and eject particles at the sediment-water interface (“conveyor-belt feeders”; Rhoads, 1974). The effective or total bioturbation in reefal environments largely depends on the kinds of organisms present as feeding mode, frequency, and behavior dictate the type of the sediment

mixing. The process of bioturbation is regarded as part of early diagenesis as it contributes to altered physical and chemical sediment nature and structure (e.g., Soetaert et al., 1996). Hence, bioturbation affects sediment biogeochemistry, including organic matter mineralization, oxygen, nutrient, and sulfur cycling as well as oxic and anoxic mineralization (e.g., shell dissolution, Fe and Mn reduction). Therefore, the following discourse discusses some of the most important aspects of bioturbation in reefal environments including the effects of bioturbation on (1) sediment sorting, (2) depth of mixing, (3) time-averaging and preservation potential (i.e., shell age, shell loss, including corrosion and dissolution), and (4) geochemical composition and the oxygen/redox potential within the uppermost sediment layer.

### Effects of bioturbation on sediment sorting and texture

Sediment composition in most reefal environments is dominated by carbonate material originating from local sources. Hence, grain or particle size distributions are poor indicators of hydrodynamic regimes but rather represent the skeleton-producing plants and animals present. Although hydrodynamic sediment sorting takes place in shallow water and within wave-influenced water depths, affecting grains of various buoyancies (e.g., porous *Halimeda* flakes, sea urchin shells or solid molluscs shells), bioturbation appears to have a much more profound impact on sediment sorting and texture. In fact, on the Great Barrier Reef, Australia, several studies have shown that surface sediments in reef lagoons show only short-term sediment sorting due to tropical cyclone activity. Surface sediments became slightly “coarser” following cyclones but reverted to their pre-storm appearance within a few weeks as a result of bioturbation activity (Carter et al., 2009; Gagan et al., 1988; Riddle, 1988).

In reefal environments, typical bioturbators include crustaceans, annelid worms (polychaetes, oligochaetes, etc.), gastropods, bivalves, holothurians, fish, and many other infaunal and epifaunal organisms, which burrow, feed, and rework particles in the uppermost sediment layers. While some of these mainly ingest loose sediments (e.g., worms, holothurians, and fish), they may be responsible for significant sediment mixing as surface sediment turnover rates have been estimated to be as high as 650 kg/m<sup>2</sup>/year (Scoffin, 1992). Although it is difficult to determine absolute sediment turnover and bioturbation rates, the process of bioturbation can lead to significant sediment mixing and sorting. For example, conveyor belt deposit-feeding organisms prevalent in both marine and freshwater systems ingest sediments over a range of depths while depositing gut contents above the sediment surface. This action results in particle-selective transfer of buried materials to the sediment surface and imposes an accelerated rate of sediment and pore water burial within the feeding zone (Robbins, 1986). In the Gulf of California, this sediment sorting activity and the creation



of biogenic stratification by polychaetes forms a distinctive type of biologically produced bedding with fine-grained material 20–40 cm thick overlying coarser material (Meldahl, 1987). Other organisms can also create graded bedding through preferentially moving sediment grains of a particular size, shape, density, or composition.

One of the best-documented bioturbators is callianassid shrimp. These burrowing organisms construct and maintain burrows with species-specific architectures. They ingest sediment material, preferentially, burying gravel-sized grains effectively, sorting sedimentary deposits based on grain size (Bradshaw and Scoffin, 2001; Branch and Pringle, 1987; Meldahl, 1987; Tudhope and Scoffin, 1984; Ziebis et al., 1996). In the Great Barrier Reef region, sediments finer than 1–2 mm are selectively ejected from callianassid burrows and maintained in the surface layer, whilst sediments coarser than 1–2 mm are generally transported to depths between 20 and 60 cm (Tudhope and Scoffin, 1984). Studies from Davies Reef (Tudhope and Scoffin, 1984) and Rib Reef (Kosnik et al., 2009) showed that the top 20 cm contain <10 wt-% particles >4 mm, whilst sediments at 40 cm depth have ~35–40 wt-% particles >4 mm. Hence, the surface sediments are often well sorted, fine grained carbonate debris overlying coarse-grained, poorly sorted, gravely carbonate material. In South Africa, a field study of *Callianassa kraussi* using stained sediments showed that sediment turnover rates were ~60% down to 30 cm depth within 30 days (Branch and Pringle, 1987) demonstrating their effectiveness and high bioturbation rates in reefal sediments. This sediment sorting process means that sediment samples collected from the top ~30 cm on reef platforms are generally poorly representative of the underlying sediments and are not reflective of the accumulating sediments likely to become the fossil record.

Besides sorting sediment, many organisms (e.g., fish, holothurians) also fragment skeletons during feeding. The particle fragmentation and the sediment sorting by burrowing activities lead to selective preservation of the large infaunal skeletons and continuous attrition of the finer (commonly originally framework-derived) sediment. This has been observed by several studies (Bradshaw and Scoffin, 2001; Perry, 1998) such as the work from Davies Reef (Great Barrier Reef, Australia), where pristine bivalves and corroded coral fragments were found side by side at depth (Tudhope and Scoffin, 1984). Sediment turnover by burrowers also inhibits the colonization of the sediments by other infauna or by sessile epifauna and epiflora, whereas seagrass and other rooted vegetation inhibits bioturbation.

### Depth and rate of bioturbation

Depth and rate of bioturbation (i.e., how fast sediments turnover) depends on several factors including environment (lagoon, fore reef, etc.), sediment composition and fauna and flora present. Loosely packed uppermost sediment layers favor effective bioturbation as they provide

food and shelter and yet still may present an oxygenated environment. Although several studies have focused on quantifying bioturbation rates in marine environments (e.g., Grant, 1983; Pillay et al., 2007; Shinn, 1968; Ziebis et al., 1996), little is known about bioturbation rates and depths across various reefal environments. Most bioturbators primarily affect the uppermost 40 cm of the sediment but callianassid burrows often reach depths greater than 2–3 m (Tudhope and Scoffin, 1984; Ziebis et al., 1996). A study from the tropical US Virgin Islands documented the quantity of sediment material being funneled into the subsurface galleries and ejected by *Callianassa* to be up to 2.59 kg/m<sup>2</sup>/day (Suchanek, 1983), whilst a South African field study using stained sediments in callianassid habitats suggested that the turnover rate of sediment material is in the order of 12.14 kg/m<sup>2</sup>/day. Of this material, all of the fragments >1.4 mm remained in the subsurface. In fact, these large turnover rates pertain mainly to the uppermost 20 or 40 cm as these sediments contain the organic material that these bioturbators consume. Therefore, the uppermost 20–40 cm is almost exclusively reworked (Scoffin, 1992). On John Brewer Reef in the central Great Barrier Reef region, analysis of <sup>210</sup>Pb associated with finer sediment fractions showed an actively mixed layer down to ~50 cm (with activity peaking at 19–22.5 cm) and a less actively mixed region from 50 cm to just over a meter (Walbran, 1996).

### Time-averaging and preservation potential in reefal environments

In carbonate environments, bioturbation and the size-selective sediment mixing profoundly influence the geochronological framework and thus bias the age structure of sedimentary deposits. The geochronological framework of carbonate sedimentary sequences in reefal environments is often determined based on relatively few samples, usually one biological specimen per characteristic layer and sometimes the species vary between the selected layers. However, the size-selective process of bioturbation, in particular rapid shell burial, may significantly skew shell preservation (i.e., sediment age structure) as microboring algae, fungi and other organisms, as well as chemical dissolution are most effectively at or very close to the water-sediment interface. This is why many taphonomic studies in the last few decades have focused on a better understanding of the issue of time-averaging as the age structure of modern sedimentary deposits are critical to understand for any study of past and modern sedimentary systems, processes, ecological evolution, etc. (Carroll et al., 2003; Flessa et al., 1993; Kidwell, 2001; Kosnik et al., 2009; Kosnik et al., 2008; Kowalewski, 1996; Meldahl et al., 1997; Staff et al., 1986).

Time-averaging is the range of ages represented in a sample and determines the length of time represented by a stratigraphic unit, and it determines the temporal resolution of a given sedimentary record (Flessa et al., 1993;

Kowalewski, 1996). Time-averaging is fundamentally determined by three largely independent parameters: (1) the rate of sediment accumulation; (2) the characteristics of sediment mixing; and (3) the durability of the individual biological constituents being averaged (Kosnik et al., 2009; Tomasovych and Zuschin, 2009). The sedimentation rate determines the minimum possible degree of time-averaging and in general, higher rates of sedimentation lead to less time-averaging. Rate and depth of mixing determines often the maximum possible time-averaging and deeper and faster sediment mixing leads to more time-averaging (e.g., callianassid shrimps, which effectively sort sedimentary grains by size, shape and/or other characteristics) (Branch and Pringle, 1987; Tudhope and Scoffin, 1984). Durability determines the length of time that a sedimentary grain or fragment remains intact and recognizable. Fragile sedimentary grains/fragments are more likely to be destroyed (i.e., eroded, or dissolved) during mixing leading to less time-averaging, whereas durable grains can be thoroughly mixed without breaking leading to more time-averaging (Kosnik et al., 2009). Taxa with different taphonomic characteristics are, therefore, likely to withstand different intensities of mixing before breaking, and therefore record different amounts of time-averaging even within the same sedimentary deposit. The potential for differential time-averaging has important implications not only for the age model of the deposits but also for the creation of death assemblages and the formation of the fossil record (Cummins et al., 1986; Perry, 1998; Tomasovych and Zuschin, 2009).

It is well known that pre- and post-burial concentrations of skeletal remains pose problems for assessing population densities of individual species, in particular, the recognition of sharp changes in abundance (including plague outbreaks). For example, studies of the abundance of the skeletal elements of the crown-of-thorns starfish *Acanthaster planci* in Great Barrier Reef sediments (Moran, 1992; Walbran et al., 1989a) showed that bioturbation of the sediment is too great to recognize individual historical outbreaks. A similar study following the mass mortality of the Caribbean reef urchin *Diadema antillarum* in 1983 showed that the fossil record of Antillean *Diadema* offers no clues as to whether die-offs had occurred in the ancient past (Greenstein, 1993). Despite the fact that for several weeks immediately after the 1983 mass mortality Caribbean reefs were littered with the long black spines and disarticulated calices of this echinoid, less than a year after the event, the sedimentary record contained no evidence of a marked increase in the remains of *Diadema* (Greenstein, 1991). This may have been the product of the limited sampling method applied or more likely, the extent of physical and biological reworking and chemical breakdown of *Diadema* skeletal elements. In a theoretical approach, it has been suggested that the assessment of the abundance of a species in the fossil assemblage is impossible to determine until the indices are scaled with the indices of other faunal constituents (Pandolfi, 1992). Indices should also be calculated at

several different size classes to provide information on depositional and taphonomic processes.

Species, size, and composition-dependent preservation and mixing potential and its subsequent implication for carbonate sediment composition in reefal environments has received new attention with the advent of amino-acid racemization dating techniques, that, when combined with radiocarbon methods, enable large numbers of specimens to be dated (e.g., Carroll et al., 2003; Kidwell et al., 2005; Kosnik et al., 2007; Kosnik et al., 2009; Kosnik and Kaufman, 2008; Kosnik et al., 2008). The study from the mixed carbonate-siliciclastic shelf of Brazil looking at calcitic brachiopod shells (*Bouchardia rosea*) from four different locations showed that the dated shells vary in age from modern to 3,000 years, with a standard deviation of 690 years (Carroll et al., 2003). The data from four localities displayed significant differences in the range of time-averaging and the structure of the age distribution (i.e., scale and mixing of the sediment columns), implying that environmental factors and local fluctuations in populations of shell-producing organisms are the principal determinants of time-averaging in marine benthic shelly assemblages.

The study of the Rib Reef (Great Barrier Reef, Australia) lagoonal sediments documented significant half-life differences between large and small *Tellina* bivalve shells (Kosnik et al., 2007). There, the top 20 cm of sediment contained almost exclusively living bivalves whilst the sediments in the subsequent 100 cm depth were homogeneously mixed. The youngest shell age at 120 cm depth was 33 years whilst at 30–35 cm depth, the oldest shell was very old (~4,680 years). In addition, comparisons of age distributions and shell half-lives of four molluscan taxa (*Ethalia*, *Natica*, *Tellina*, and *Turbo*) from Rib Reef supported these findings (Kosnik et al., 2009). There, the 428 dated shells displayed the same homogeneous shell stratigraphy below 20 cm depth. Shell half-lives did not coincide with any single morphological characteristic thought to infer greater durability, but correlated to a combined durability score based on shell density, thickness, and shape. The half-lives of the four taxa ranged between ~575 years (*Tellina*) and 1,230 years (*Turbo* opercula). Interestingly, whilst the Rib Reef studies showed a distinct top layer and a deeper age-homogeneous layer, other studies using radiocarbon ages of the bulk carbonate sediments have found stratigraphic consistency, for example, on neighboring John Brewer Reef (Walbran et al., 1989b), but investigations using  $^{210}\text{Pb}$  (associated with finer sediment fractions) also showed that the top 50 cm were actively mixed, whilst the next 50 cm were less mixed (Walbran, 1996).

The study from Caribbean reefal environments in Panama (Kidwell et al., 2005) compared time-averaging and bivalve shell loss in both carbonate and siliciclastic environments and showed that siliciclastic sands and muds contain significantly older shells (median, 375 year, up to ~5,400 years) than nearby carbonate seafloors (median 72 year, up to ~2,900 year). This led to the conclusion that

shell loss rates in carbonate environments are greater as a result of bioerosion and dissolution, which implies greater compositional bias in the surviving skeletal material and leads to the taphonomic trade-off that shells in carbonate sediments show less time-averaging but greater taxonomic bias. Similarly, other studies from Panamanian and the Belize Barrier Reefs also demonstrated the high level of shell damage and dissolution compared to shells in other environments (Best, 2008; Hauser et al., 2009).

The results of these time-averaging studies demonstrate that bioturbation-related selective shell burial favors shells that remain buried through their early taphonomic history. Although buried shells may be brought back up to the surface intermittently by bioturbation or physical reworking (e.g., storms, currents), this exposure is often only for short periods of time. This taphonomic model explains the striking similarities in time-averaging among different types of organisms and the lack of correlation between time-since-death and shell taphonomy. Hence, age estimates in these depositional settings are sensitive to taxon choice and quantify a taxon-dependent bias in shell longevity and death assemblage formation. Most importantly, these conclusions of stratigraphic disorder are not restricted to modern carbonate reefal sediments as studies from other environmental settings, such as tidal flats, etc. have demonstrated (e.g., Best, 2008; Flessa et al., 1993; Tomasovych and Zuschin, 2009). In summary, greater understanding of biases imposed by bioturbation on preservation will ultimately be key to understanding apparent contradictions in modern and past sedimentary records (see also O'Leary et al., 2009).

### Geochemical aspects of bioturbation

Vertical transport and surface sediment mixing mechanisms also profoundly influence biogeochemical processes, microbial communities and hence early diagenesis (e.g., Alongi, 1989; Berner, 1980; Pischedda et al., 2008). In carbonate environments, dissolution of carbonate grains is highest in extensively bioturbated areas (e.g., Aller, 1982; Callender et al., 2002) or very close to the sediment-water interface (Tudhope and Risk, 1985) where oxygen is abundant. Chemical dissolution of particles is accelerated by microboring algae and fungi, which are abundant in coral reef environments. A dissolution study from Davies Reef (Great Barrier Reef, Australia) showed that molluscan shells lost 3% weight over 1 year. Such rates equate to 350 g of dissolved  $\text{CaCO}_3/\text{m}^2$  lagoonal floor/year and represent 18–30% of the sediment influx rate during the Holocene (Tudhope and Risk, 1985).

Bioturbation and bioirrigation (e.g., the exchange of water masses) largely controls the penetration depth of oxygen and organic material into the surface sediments, whilst the consumption of oxygen is influenced by respiration of the benthic organisms as they oxidize organic carbon. In contrast, anaerobic oxidation is almost exclusively mediated by bacterial activity (Berner, 1980). In

reef sediments of Davies Reef (GBR, Australia), sulfate reduction accounted only for 5% of the total organic matter degradation within the top 12 cm with reduction rates averaged  $0.622 \text{ mmol sulfate m}^2/\text{day}$  (Nedwell and Blackburn, 1987). The importance of the biogenic dwellings and structures in carbonate sediment environment lies in the creation of three-dimensional mosaics of oxic/anoxic interfaces in the sediments thus multiplying by several times the volume of the oxygenated sediment (e.g., Kristensen, 2000). Several field and laboratory studies showed that sediment reworking and burrowing activities extended the depth of the oxidized zone (see, for example, Krantzberg (1985) for summary) and are able to create oxidized microenvironments below the aerobic zones (e.g., Myers, 1977; Ziebis et al., 1996). The various bioturbation organisms in reefal environments have distinct bioturbation behavior patterns, which create oxygen distribution heterogeneity. It has been shown that the gallery-builders produced greater spatial heterogeneity due to their complex ventilated structures compared to the burrower species (Pischedda et al., 2008). Moreover, oxygen distribution heterogeneity affects the diffusive oxygen flux as organisms enhance the oxygen exchanges between water and sediments (Ziebis et al., 1996). This outweighs the reduced oxygen flux due to the physical presence of organisms in the biogenic structures or the deposition of mucus along the borrow walls by worms, etc., which may act as a barrier to solute diffusion (Hannides et al., 2005). Furthermore, the process of bioturbation and bioirrigation also actively influences other conditions, such as pH, nutrient status, ammonia, phosphorous, nitrate, and metals contents (see Krantzberg (1985) for summary). Alteration of the diffusive oxygen flux through bioturbation processes by dwelling benthos, such as conveyor-belt feeders or the callinassid shrimps (Ziebis et al., 1996), may also dramatically influence mineralization processes in sediments. Additionally, bioturbation affects biogeochemistry including organic matter mineralization, nutrient and sulfur cycling as shown by a study from the Philippines of alpheid shrimps *Alpheus macellarius* (Holmer and Heilskov, 2008). There, high sediment turnover rates by the shrimps stimulated the mineralization rate.

### Summary and conclusion

Bioturbation refers to particle mixing within unconsolidated sediments through the activities of biological organisms most commonly at or close to the water-sediment interface. In reefal ecosystems, the implications of this process go far beyond simply mixing the substrate as sediment particle preservation, food availability, and geochemical composition within the substrate are all affected, including increasing the effective sediment-water interface that enhanced chemical fluxes (i.e., oxygen, nutrients, sulfur cycling, oxic and anoxic mineralization) between the sediment and the water column. The effective or total bioturbation, part of early diagenesis processes, largely



depends on the kinds of organisms present as feeding mode, frequency and behavior dictates the type of the sediment mixing. The process of bioturbation, therefore, critically impacts reef ecosystems as it influences (1) sediment sorting, (2) depth of mixing, (3) time-averaging and preservation potential (i.e., shell age, shell loss, including corrosion and dissolution), and (4) geochemical composition and the oxygen/redox potential within the uppermost sediment layer.

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## Cross-references

Algae, Coralline  
 Bioerosion  
 Calcite  
 Carbon Fluxes of Coral Reefs  
 Carbonate Budgets and Reef Framework Accumulation  
 Classification of Carbonates  
 Coral Reef, Definition  
 Density and Porosity: Influence on Reef Accretion Rates  
 Diagenesis  
 Eco-Morphodynamics  
 Forereef/Reef Front

Fringing Reefs  
 Geomorphic Zonation  
 Halimeda  
 Holocene Reefs  
 Intrinsic and Extrinsic Drivers on Coral Reefs  
 Lagoons  
 Micrite  
 Porosity Variability in Limestone Sequences  
 Reef Flat  
 Reefal Sediments  
 Reef Structure  
 Sediment Durability  
 Sediment Dynamics  
 Sediments, Properties

## BLOWHOLES

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### Definition

A blowhole is a crack or fissure in coastal rock through which air and spray is expelled when waves break on the shore.

Blowholes are a feature where large swell impacts coasts, on which the rock contains fractures. Weaknesses, such as joints or fault lines, are preferentially widened, primarily through wave action but also through other processes such as solution of reef limestone. In many cases this can result in a sea cave. Coasts that experience strong swell are impacted by trains of regular period waves generated by remote storms and which have travelled across the ocean. Successive waves trap air into the fissure or sea cave and compress it as the crest of the wave fills the cavity. This pneumatic pressure is released in a spectacular fashion with a deep hiss and an upward spray or blast of water through the cracks [Figure 1](#).



**Blowholes, Figure 1** Several adjacent blowholes on the southern shore of Tongatapu, Kingdom of Tonga.

Blowholes can occur on coasts that are composed of a range of lithologies, and there are a number of swell-dominated coasts on which these regular spouts of spray are a tourist attraction. Lava tubes and dykes can give rise to suitable fissures on volcanic coasts, such as the Taga or Alofaaga Blowholes on Savai'i in Samoa, or Halano Blowhole on Oahu and a blowhole at Nakalele Point on Maui in the Hawaiian Islands. Blowholes are also associated with Tertiary limestones on reef coasts. Where the coast is not protected by a modern reef, spectacular blowholes occur, for example, on the southern shore of Tongatapu, the principal island in the Kingdom of Tonga, and at the eastern end of Grand Cayman, the largest island in the Cayman Islands.

## BLUE HOLE

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Blue holes are underwater karst caves, which when found in shallow water, have striking features because of the strong color contrast between the dark blue cave opening and the light blue surrounding seafloor. A classic modern example is the blue hole in the lagoon of the Lighthouse Reef Atoll in Belize (Figure 1). This blue hole is cylindrical in shape, has a diameter of 300 m and is 120 m deep. It was formed by subaerial dissolution of Pleistocene reef limestone during glacial sea-level lowstands and later roof collapse (Dill, 1977). Giant stalactites found in 40 m depth are impressive evidence of the subaerial cave formation.

Because the lower water column of this blue hole is anoxic, fine-grained bottom sediments turned out to be undisturbed and annually layered. They were used as high-resolution Holocene climate archive (Gischler et al., 2008). Other prominent examples include the blue holes of the Pompey reefs in the Great Barrier Reef of Australia (Backshall et al., 1979), the “puit sans fond” of Clipperton Atoll in the eastern Pacific (Sachet, 1962), the black hole of Andros Island, Bahamas (Schwabe and Herbert, 2004), or the blue hole of Dahab at the fringing reef coast of the Gulf of Aqaba in the northern Red Sea. Even though their depths do not exceed 35–40 m, both the Clipperton and the Andros holes have anoxic bottom water bodies, though the bottom sediments have as yet not been investigated. The depths of the Pompey reef blue holes are also not greater than 40 m and the bottom sediments are coarse-grained. The Dahab blue hole is 100 m deep; scientific studies are missing. The Blue Hole terrains of the Houtman Abrolhos reefs, Western Australia, were recently identified to be growth structures rather than karst features (Wyrwoll et al., 2006). Blue holes may also have more irregular shapes as documented by the many modern examples in the Bahamas (Dill, 1977; Gascoyne et al., 1979). Elongated caves are often related to tectonic structures such as faults and joints that acted as conduits of circulating fresh water during subaerial exposure. Fossil examples of these elongated structures are termed neptunian dikes. They were first described by Fischer (1962) from the Triassic of the Calcareous Alps and are meanwhile known from reefs and carbonate platforms in virtually all Phanerozoic systems. Interestingly, there are several examples of both modern and fossil reefal submarine caves and neptunian dikes that host microbial (“stromatolitic”) structures (e.g., Taylor and Palmer, 1994). Their formation may be explained by the



**Blue Hole, Figure 1** Aerial photograph of the Lighthouse Reef Blue Hole, Belize. The hole is 300 m across and surrounded by a patch reef ring that is interrupted at two locations.



special environments met in caves that can be related to water chemistry (e.g., elevated carbonate concentration), anoxia, low light intensity, lack of physical disturbance, or exclusion of grazing metazoa.

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## Cross-references

[Atolls](#)  
[Lagoons](#)  
[Sclerochronology](#)

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## BOAT CHANNEL

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## Synonyms

Back-reef trough or tide pool; Moat; Shallow lagoon

## Description

There are two types of boat channels. Artificially constructed boat channels are dug, dredged, or blasted through a reef to allow access to land or wharf facilities. Such channels are usually cut normal to the reef edge or at an oblique angle and require continual maintenance. Natural boat channels, and the ones described in classical reef literature, are depressions that run parallel to the shore and are

generally associated with the back reef area of fringing reefs. Darwin (*Darwin, Charles (1809–1882)*) described an example from Mauritius as a flat space with sandy bottom, located between the outer margin of the fringing reef and the island shore, the depression being sufficiently deep to offer “a safe coasting channel for boats.”

To Darwin the reason for a boat channel was clear; a reef on a sloping surface would at first grow up some distance from the shore, and, because coral on the outer edge would grow much more vigorously than those inshore, a “flat space” would form behind. Others have suggested a more dynamic process, where water driven across the fringing reef by waves and currents, flows laterally out through the boat channel maintaining its form. Because the channels fail to drain completely at low tide they are frequently colonized by marine grasses, algae, and sometimes corals.

Not all fringing reefs have boat channels. Those that do have a myriad of length, width, depth, and continuity scales fully described by Guilcher (1988) with examples of incipient forms from the Gulf of Aquaba, intermediate forms from the Seychelles and Sri Lanka, and well developed forms from Madagascar, New Caledonia, and Lord Howe Island.

Narrow boat channels are also known from atolls and table reefs where they separate the island shore from the reef flat, do not drain completely at low tide, and generally have sparse coral cover because of sediment movement. Such channels are also known as *Moats*.

In a recent review of fringing reef growth and morphology Kennedy and Woodroffe (2002) prefer the less archaic and less ambiguous term “shallow lagoon” rather than boat channel for the back reef depression on fringing reefs. And, they provide details of the 2 km wide and 1.5 m deep shallow lagoon on Lord Howe Island.

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## Cross-references

[Fringing Reef Circulation](#)  
[Fringing Reefs](#)  
[Moating](#)  
[Moats](#)

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## BOULDER BEACHES

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## Synonyms

Coarse clast beaches; Gravel beaches; Storm beaches



**Boulder Beaches, Figure 1** Boulder beach at Iris Point, Orpheus Island, North Queensland. Photo by D. Hopley.

### Definition

Boulder beaches occur along many of the world's coasts. Their presence and formation is a function of sediment availability and wave energy. Both storm waves and tsunami may be responsible for deposition of boulder beaches but differentiating which of the two may have been responsible, principally, at any one location can be difficult (Nott, 2004). It is common for boulder beaches to display sorting both alongshore but more often perpendicular to the shore with coarser clasts closer to the intertidal zone and progressively fining with distance landward (Figure 1). The shape of clasts varies depending upon the nature of the bedrock from which the clasts were derived and also the depositional processes. Joint spacing in the source bedrock will often limit clast size. Lithology along with the history of transportation and reworking will influence the degree of abrasion and eventual clast shape. Clasts that have experienced a high frequency of reworking and mobilization will theoretically be more rounded whereas clasts that have experienced only one transporting event after erosion from their bedrock source could be expected to be more angular. However, in this last instance the degree of angularity will depend upon the nature of that bedrock source i.e., whether it was composed of rounded core stones in a saprolitic profile or was unweathered jointed rock.

The age of boulder beaches can vary. Hopley and Barnes (1985) identified a potential Pleistocene boulder beach on Orpheus Island, Queensland. Hopley (1984) suggested that many of the boulder beaches on islands and the mainland coast adjacent to the Great Barrier

Reef could have developed during the Holocene high-energy window (8–6.5 kyr) when higher energy swells were able to penetrate into the lagoon of the Great Barrier Reef before reefs had reached sea-level. Other boulder beaches in Queensland are younger than this. Nott (2003) dated coral fragments buried within boulder beaches and found that they were deposited or at least reworked substantially over the past few hundred years. Nott (2003) attributed these accumulations to deposition or reworking by tropical cyclone induced marine inundations.

One of the key and important aspects of boulder beaches in tropical regions is that they can form the substrate for coral reef growth. Hopley and Barnes (1985) observed a fringing coral reef growing on an accumulation of well rounded spherical to oblate shaped lithic boulders 30–40 cm in diameter at Iris Point on Orpheus Island, Queensland. Perry and Smithers (2009) also describe corals colonizing a boulder beach at Stingaree Reef, Queensland. Here these authors suggest the corals grow laterally stabilizing the substrate via “meniscus type bridges” and eventually coalesce with other corals growing on other boulder clasts. It is likely that many boulder beaches appear to have been stabilized by coral reef growth during the Holocene transgression.

In summary, boulder beaches record episodes of changed environmental conditions and high intensity events throughout the Holocene. They can vary in age from Pleistocene to recent and their colonization by coral reefs highlights that reefs do not need initially stable substrates upon which to grow.

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## Cross-references

[Fringing Reefs](#)  
[Holocene High Energy Window](#)  
[Tropical Cyclone/Hurricane](#)  
[Tsunami](#)

## BOULDER ZONE/RAMPARTS

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### Definition

Larger than shingle (20–200 mm in diameter), a boulder is a rock detached from the parent body with size ranging from 256 mm to several meters in diameter. Some degree of rounding has characteristically taken place through abrasion during transport (Carr, 1982).

In coral reef areas, a boulder rampart is a narrow ridge of boulders thrown up along part of the edge of the reef flat, especially on the side from which the prevailing winds blow. The rampart, which should not exceed 1 or 2 m in height, may however reach as much as several meters in some cases (Figure 1). It occurs close behind the lithothamnion (now referred to as *Porolithothamnion*) ridge where it is present (Howell, 1957). In older ramparts that became lithified (Figure 2), the size of boulders, larger than the smaller debris forming a coral conglomerate, is often still recognizable. In areas affected by tropical storms (hurricanes, typhoons, cyclones) the size of the boulders and of the ramparts may increase, and it may be difficult to distinguish them from those left by a major tsunami (e.g., Scheffers, 2005).

Recently, coral-reef bleaching is drastically reducing the coral populations in several areas. Thus skeletal coral



**Boulder Zone/Ramparts, Figure 1** An impressive boulder zone is developed along most of the southern coast of the small (1 km<sup>2</sup>) Tromelin Island (French “Iles Eparses,” Indian Ocean). The outer rampart may reach over 6 m in height and is formed by white boulders left by recent storms. In the upper part of the rampart the boulders are already blackened by Cyanophycean algae, indicating less recent storm deposits. A folded double meter gives scale (15°53′.59 S–54°31′.70 E, May 2009).



**Boulder Zone/Ramparts, Figure 2** Remnant of an ancient boulder rampart, now lithified, reaching 1.9 m above sea level on the north coast of Temoe atoll (French Polynesia). Two coral samples collected at 1.5 and 0.6 m above sea level, have been dated by radiocarbon 3,405 ± 85 year BP (Hv-12667) and 2875 ± 85 year BP (Hv-12668), respectively. At that time sea level was about 0.8 m above present (Pirazzoli, 1987) (photo # 7430, Oct. 1982).

materials are reduced, disrupting the process of forming and maintaining certain boulder ramparts (Williams et al., 1999). The term boulder ramparts, has also been used in glacial areas, indicating deposits left by debris-laden sea ice or by wave-washed remnants of old glacial moraines (e.g., Schwartz, 2005).



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## Cross-references

Algal Rims  
Boulder Beaches  
Conglomerates  
Platforms (Cemented)  
Shingle Ridges  
Tropical Cyclone/Hurricane  
Tsunami

## BRAZIL, CORAL REEFS

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## Synonyms

Coral Reefs of the Southwestern Atlantic

## Definition

Brazil: The largest country in the South American continent, with an area of 8,512,000 km<sup>2</sup> and a coastal zone that extends for approximately 9,200 km.

Brazilian coral reefs: The southernmost reefs of the Western Atlantic Ocean.

## Introduction

French biologist Jacques Laborel (1969, 1970) published the first comprehensive description of the Brazilian reefs. Earlier nineteenth century reports by visiting scientists such as Darwin (1851), Hartt (1868a, b, 1870), and Rathbun (1876, 1878) described the unusual characteristics of the Brazilian reefs: their almost unique mushroom-like growth forms (chapeirão) and the strong endemism and low diversity of the coral fauna. Interest in the studies of Brazilian reefs has increased over the last two decades for several reasons: an increasing number of Brazilian researchers have been studying reefs; reef areas have become increasingly degraded; and Brazilian reefs

have been recognized as an important example of reef growth under marginal environmental conditions. Recent research has included more detailed surveys of the reef environment and the analysis of quantitative databases in numerous articles, theses, and dissertations, as well as technical reports. These publications mainly describe the coral fauna, its endemism, and the adaptation of a low diversity fauna to a highly siliciclastic muddy environment; the fauna and flora of the reef communities; the classification and distribution of the major Brazilian reef systems; the aspects that influenced the Quaternary evolution of these reef systems; and the conservation, protection, and management of these reefs, including reviews of the major natural and anthropogenic impacts that threaten Brazilian coral reef ecosystems.

## Regional setting

The Brazilian coastal zone presents a very diverse suite of environments that evolved during the Quaternary period in response to climate and sea level changes. These evolutionary changes were controlled by variations in the sediment supply and a geological heritage dating to the Gondwana break up in South America and Africa during the Mesozoic period. During the Quaternary period, changes in the relative sea level and climate added younger morphological elements such as tidal flats, wetlands, coastal dune fields, and coral reefs to the coastal zone (Dominguez, 2009).

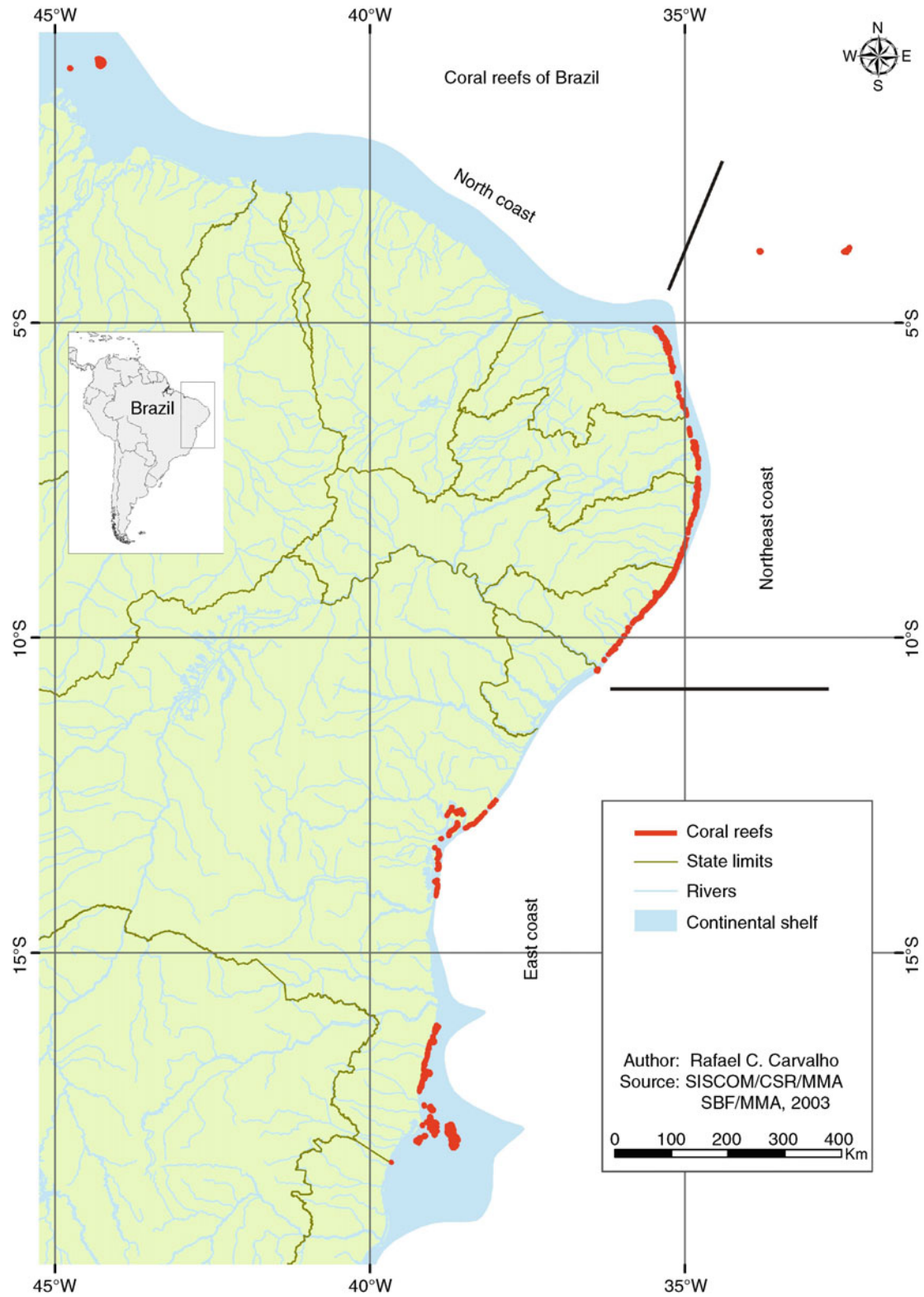
The continental shelf along the tropical coast of Brazil has a relatively low relief and is very narrow (an average width of 50 km), extending up to 200 km at its southern portion and forming the Royal Charlotte and the Abrolhos banks. The shelf break occurs between depths of 60 and 80 m. Tidal variation range from micro- to meso-tides, with spring tides varying from 1.7 m at the southernmost region to 3.0 m at the extreme north.

According to Bittencourt et al. (2005), the most significant wave front directions are northeast, east, southeast, and south-southeast. North and east waves have periods of 5 s and heights of 1.0 m, while southeast and south-southeast waves have periods of 6.5 s and heights of 1.5 m.

Coral reefs are primarily distributed along the northeastern and eastern Brazilian coast and are less common on the continental shelf in the northern part of the country, a region influenced by muddy sediments from the Amazon River (Figure 1). Nearshore shallow banks and fringing reefs are common within siliciclastic sandy and muddy sediments, and offshore reefs are located in a carbonate-dominated province (Leão et al., 2003).

## Reef-building coral fauna

The Brazilian coral fauna (Scleractinia) has three distinctive characteristics: (a) it has a very low diversity coral fauna (21 species) compared with that of the Caribbean or the Indo-Pacific reefs; (b) the major reef builders are

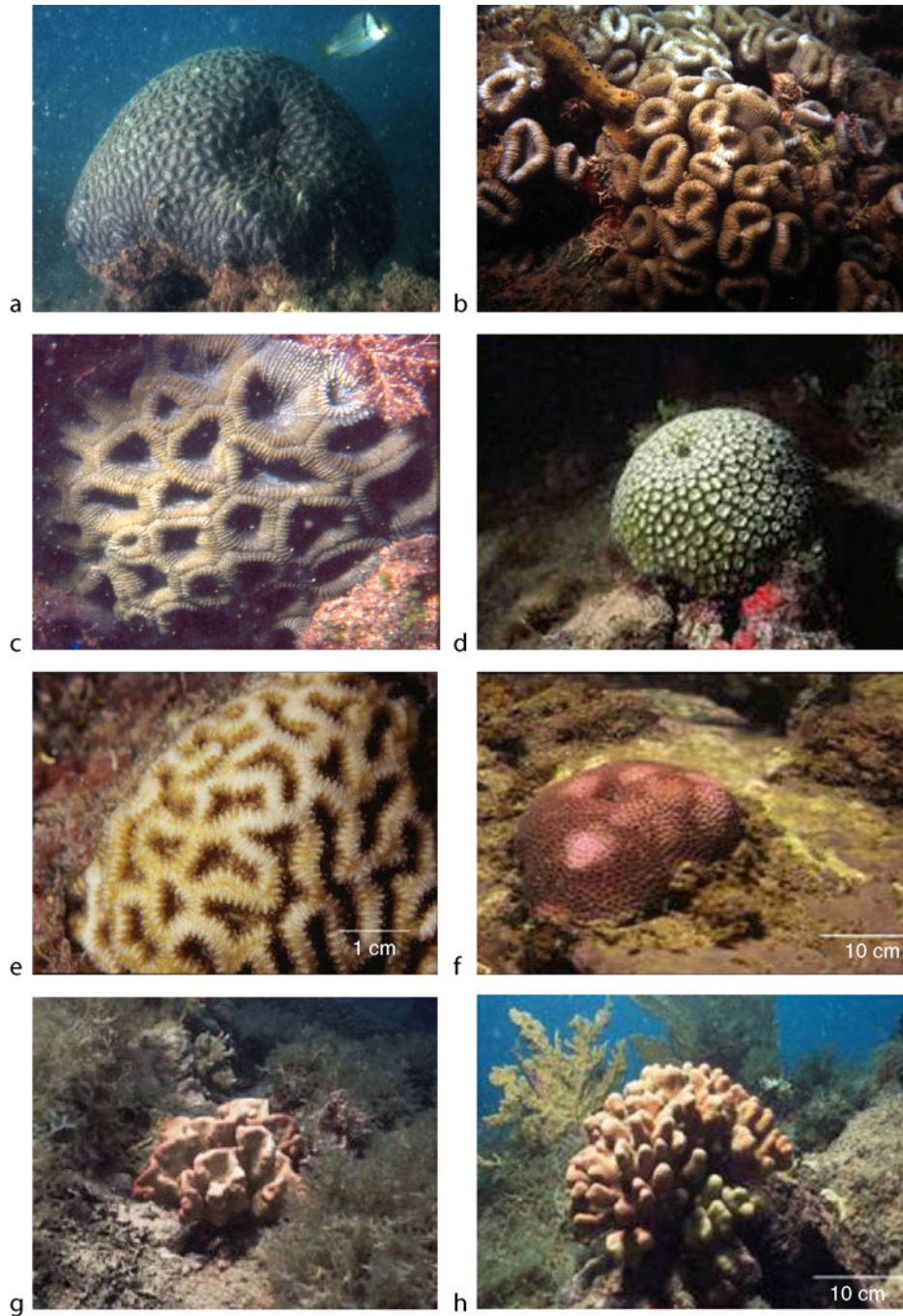


Brazil, Coral Reefs, Figure 1 Location of major coral reef areas in Brazil.

endemic species from Brazilian waters; and (c) it is predominantly composed of massive corals.

Six of the reef-building Brazilian corals are endemic and some of these species are related to recent Caribbean coral forms while others are related to a Tertiary coral fauna. The archaic species are the most common corals in most modern Brazilian reefs and include the three

species of the genus *Mussismilia*: *M. braziliensis*, *M. hispida*, and *M. hartti*, as well as the species *Favia leptophylla* (Figure 2a–d). The other two endemic species are *Siderastrea stellata* and *Favia grvida* (Figure 2e and f), which are both related to the present Caribbean coral fauna. *M. braziliensis*, *M. hispida*, and *Siderastrea stellata* are found among the massive main frame builders.



**Brazil, Coral Reefs, Figure 2** Endemic Brazilian coral species. (a) *Mussismilia braziliensis*; (b) *Mussismilia hartti*; (c) *Mussismilia hispida*; (d) *Favia leptophylla*; (e) *Favia grvida*; (f) *Siderastrea stellata*; (g) *Millepora braziliensis*; and (h) *Millepora nitida*.



*Mussismilia harttii*, very abundant in most of the reefs, has corallites in dichotomous groups with separated calyces, but does not make branches. *Mussismilia braziliensis* and *Favia leptophylla* show the greatest geographical confinement because they occur only along the eastern Brazilian region. *Mussismilia hispida* has the largest spatial distribution and is found from the northern to the southern regions of Brazil. *Siderastrea stellata* and *Favia gravida* are the most common corals in shallow intertidal pools of the reef tops. The cosmopolitan *Porites astreoides*, *P. branneri*, *Agaricia agaricites*, *A. fragilis*, *Montastrea cavernosa*, and *Madracis decactis* are common in Brazilian reefs. The small *Scolymia wellsii*, *Phyllangia americana*, *Stephanocoenia michelini*, *Astrangia braziliensis*, *A. rathbuni*, and *Meandrina braziliensis* do not contribute substantially to the construction of the reef structure. Recently, three other Caribbean species were described in the Brazilian reefs: *Siderastrea radians*, *S. siderea*, and *Scolymia cubensis* (Neves et al., 2006, 2008). Besides these reef corals, two invasive alien coral species, *Tubastrea coccinea* and *T. tagusensis* were recorded on rocky shores along the coast of the state of Rio de Janeiro (De Paula and Creed, 2004). These exotic corals probably arrived in Brazil on a ship's hull or oil platform in the late 1980s.

Five species of hydrocorals are described on the Brazilian reefs: *Millepora alcicornis*, an important reef-building component in Brazil, predominates on the windward borders of the reefs and is found along the entire tropical coast of Brazil; *Millepora braziliensis* (Figure 2g), found in the high energy zone, is more massive, but has flattened branches in the protected parts of the reefs; *Millepora nitida* (Figure 2h) is currently recorded only along the eastern region of Brazil. Amaral et al. (2008) described a new milleporid species, *Millepora laboreli*, in the northern region of Brazil. Aside from the milleporids, a small hydrocoral, *Stylaster roseus*, is found in the protected parts of reefs in the northeast and east. This species forms small colonies, a few centimeters high, which have a thick base covered with small pointed branches.

### Major reef types

Brazilian reefs comprise two groups of reefs: nearshore and offshore reefs. Nearshore reefs occur on the inner continental shelf and are either adjacent to the coast or are a few kilometers from the shoreline (<5 km). The reefs adjacent to the coast have, at present, part of their reef flats covered by siliciclastic sand. These reefs include fringing reefs and shallow bank reefs. The fringing reefs usually border the shore of the islands up to several kilometers, developing above the island substrate as a continuous fringe. This fringe became narrower with the lowering of the sea level that occurred in the late Holocene and, thus, shortened the reef distance from the shoreline and partially buried the back-reef lagoon. The fore-reef depths can vary from 5 to 10 m. A very shallow lagoon (1–2 m deep) is common in the back-reef area where small patch reefs

and coral knolls are observed. Meandering channels may occasionally interrupt the reef crest. The attached banks also occur adjacent to the beach but are of limited lateral (alongshore) extent. Generally these bank-type reefs do not exceed more than 1 km in length. The entire reef flat is located in the intertidal zone and no lagoon is formed. Tidal pools are common, generally of a reduced extent, say 5–10 m in width and usually not exceeding 1 m in depth. The reef front depth varies from 5 to 10 m and reef walls are generally abrupt.

Offshore reefs consist of reef structures of variable dimensions, from a few meters to 20 km, and are located more than 5 km off the coastline in various water depths. These reefs do not form a lagoon, and sediment transport occurs freely on the leeward side of these reefs. The offshore reefs include the following types of reef: coral knolls, patch and bank reefs, and coral pinnacles. Coral knolls can attain maximum dimensions and heights of a few meters, and are usually found at depths of less than 5 m. Patch reefs have lateral dimensions of tens of meters with the widths and lengths of the reefs being larger than the heights. The lateral walls may have a high relief of approximately 5 m. They are sparsely distributed over wide areas of the Brazilian inner shelf. The isolated bank reefs are reef structures which have horizontal dimensions ranging from approximately 50 m to tens of kilometers, and their heights above the sea floor vary from 10 m (shallow banks) to more than 20 m (deep banks). This reef type has variable shapes (irregular, circular, elongate, arc-like, etc.) and is controlled by its substrate or by its position relative to the present day sea level. Elongate reefs developed on the lines of beachrock - features that are widely distributed along the northeastern and eastern regions of Brazil. Larger and irregular bank reefs, such as those of the Abrolhos area which established on the topographic highs left by the erosion of older reef carbonates, are also included in this category. Most are flat-topped reefs that were truncated during low sea level stands, thereby favoring lateral rather than vertical growth. Submerged banks, a few meters high, are found in depths up to 20 m, and may be related to erosional phenomena followed by relative sea level oscillations. Distinctive isolated coral pinnacles range in height from 5 to 25 m above the sea floor, while the diameter of their tops ranges from 5 to 50 m. These reefs can be of two types: (a) columnar, where the base is equally as wide as or wider than the top of the reef; and (b) chapeirão, where the flat top is wider, sometimes over three times larger than its base. Chapeirão is a term introduced by Charles F. Hartt in 1870, which alludes to hats with broad brims. This coral growth form is unique to Brazilian reefs and consists of isolated narrow pillars whose tops are expanded laterally, resembling flat mushrooms (Hartt, 1870). Seen from above, these structures have an almost perfectly rounded shape and are easily mapped from aerial photographs. Aside from these reefs, two other types of oceanic reefs are found in Brazil: (a) shelf edge reefs that grow at the border of the continental shelf, with widths up to 3 km and a relief of 35 m at depths

of 50 m (Kikuchi and Leão, 1998). These reefs must have been initiated earlier in the Holocene at lower sea levels, and are now veneered with a deeper water community; and one atoll reef, Rocas, that has dimensions of 3.5 km by 2.5 km. Despite its small dimensions, a reef front, reef flat, and lagoon can be clearly distinguished and subdivided into discrete features. This reef mostly comprises nonarticulate coralline algal growth (Kikuchi and Leão, 1997; Gherardi and Bosence, 1999).

## Summary

Brazil has the most extensive and rich coral reefs in the Southwestern Atlantic Ocean. The reefs are characterized by their unusual growth forms, which have mushroom-shaped pinnacles that can fuse together on their tops, forming larger reefs structures that include the following: (a) shallow small isolated reefs that occur adjacent to the shoreline and often have elongated forms; (b) bank reefs off the coast that have widely variable sizes (<10 to >20 km) and shapes; (c) shallow fringing reefs which mostly border the coasts of islands; (d) open sea coral pinnacles, named “chapeirões”, which usually occur in depths greater than 20 m; and (e) drowned reefs at the middle and outer continental shelves. The coral fauna of the Brazilian reefs has a very low diversity (21 species) and a high degree of endemism. The major reef builders are relic forms, remnant of an ancient coral fauna dating back to the Tertiary, and lack completely branching growth forms. Brazilian reefs initiated growth after 8 ka BP, a notable period of coral expansion in the tropical world, but an incipient forced regression related to a sea level decrease of approximately 2–5 m during the last 6.0–5.0 ka had a significant influence on the evolution of the reef structures.

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## Cross-references

[Climate Change and Coral Reefs](#)  
[Sea Level Change and Its Effect on Reef Growth](#)  
[Sediments, Properties](#)  
[Submerged Reefs](#)  
[Western Atlantic/Caribbean, Coral Reefs](#)

## BRYOZOA

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## Synonyms

Ectoprocta; Ectoprocts

## Definitions

Bryozoa: A phylum or superphylum of aquatic (mostly marine) invertebrate animals, tiny (half-mm-sized) polyp-like individuals (*zooids*) with U-shaped digestive

tracts and occupying hardened (usually calcareous) exoskeletal chambers (*zoecia*), joined together in small to moderate-sized (cm-sized) colonies (*zoaria*). The vast majority are eucoelomate, comprising the subphylum or phylum *Ectoprocta*, so that at times the two Latin names have been used interchangeably.

Reefal bryozoans: Reef-dwelling bryozoans; bryozoans found on or within coral-reef frameworks, rubble, and flanking sediments.

### Introduction: Bryozoans in modern reefs

Bryozoans are found worldwide, from tropical to polar, and shoreline out to deep ocean. Some occur on reefs in warm shallow seas. Those colonies (Figure 1) are most often thin crusts whose upper surfaces exhibit many tiny pin-prick-like holes; other zoaria are thicker crusts or masses, flexible tufts, low-standing branches or lattices, and encrusting networks (Cuffey, 1973).

On closer examination, most of the reefal colonies can be seen to consist of short box-like zooecia and therefore belong to the order *Cheilostomida*, by far the most abundant and diversified of the living bryozoan groups (Cuffey and Utgaard, 1999, p. 208, 210). The others are made of long tube-like zooecia, representing the order *Cyclostomida* (Cuffey and Utgaard, 1999, p. 208–209, 211).

### History of discovery

In the early days of scientific study of modern coral reefs, bryozoans were overlooked by reef workers, due to their small crust-like colonies being inconspicuous compared to the larger coral heads and branches dominating reef surfaces.

In those days, taxonomic or faunal studies of bryozoans of large regions including reefs would contain scattered notes on certain species that had been found on coral or rock here and there, but not as any systematic analysis of reef-related occurrences. Examples include Egypt (Audouin, 1826), Tanzania (Ortmann, 1892), *Florida Keys* and the (Smitt, 1872–1873; Canu and Bassler, 1928; Osburn, 1940), and the Philippines (Canu and Bassler, 1929). Many such records were drawn together by Winston (1986).

Beginning about 1970, field studies specifically targeting bryozoans in living reefs revealed substantial numbers of bryozoans, particularly on the *Bermuda* and *Enewetak Atoll, Marshall Islands* (Cuffey, 1970, p. 44–45, 1972, 1973). Since then, a number of modern reefs examined for bryozoans have been found to also have significant bryozoan components, as for example the *Great Barrier Reef: Origin, Evolution, and Modern Development* (Ross, 1974; Ryland, 1974; Cuffey, 1978) among Pacific Coral Reefs (*Pacific Coral Reefs: An Introduction*), the Virgin Islands (Schopf, 1974), *Bahamas* (Cuffey and Fonda, 1977), and *Jamaica* (Jackson and Buss, 1975; Jackson and Winston, 1982) among Atlantic and Caribbean reefs.

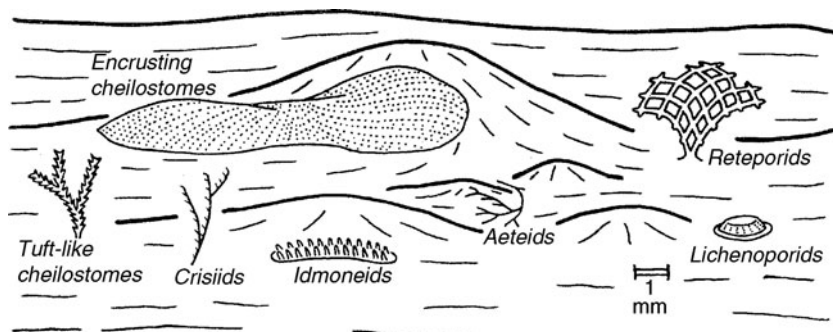
### Extension into the fossil record

Present-day types of bryozoan involvement in coral reefs go back to at least mid-Cenozoic time (approximately 30 ma). Miocene, Pliocene, and Pleistocene fossil reefs often exhibit bryozoan crusts among the corals in the same manner seen on living reefs, as figured in the Late Pleistocene (125 ka) reefs in the *Florida Keys* (Cuffey, 1977, p. 187–188) and noted in the Early Miocene uplifted atoll of *Makatea* (Cuffey and Montaggioni, 1986) and the Latest Miocene reefs in Algeria (Hamdane and Moissette, 2002).

Further back in geologic time, bryozoans occur in earlier fossil reefs or *Bioherms* and *Biostrome*, but their participation therein can be understood in terms of expansions of their roles (Cuffey, 1977) as initially defined from modern reefal bryozoans (Cuffey, 1972) (*see next section*). The Bryozoa originated long ago (Ordovician Period, early in the Paleozoic Era, roughly 475 ma), evolved into different classes and orders (some now extinct; Cuffey and Utgaard, 1999), several of which participated in reefs at various geologic times.

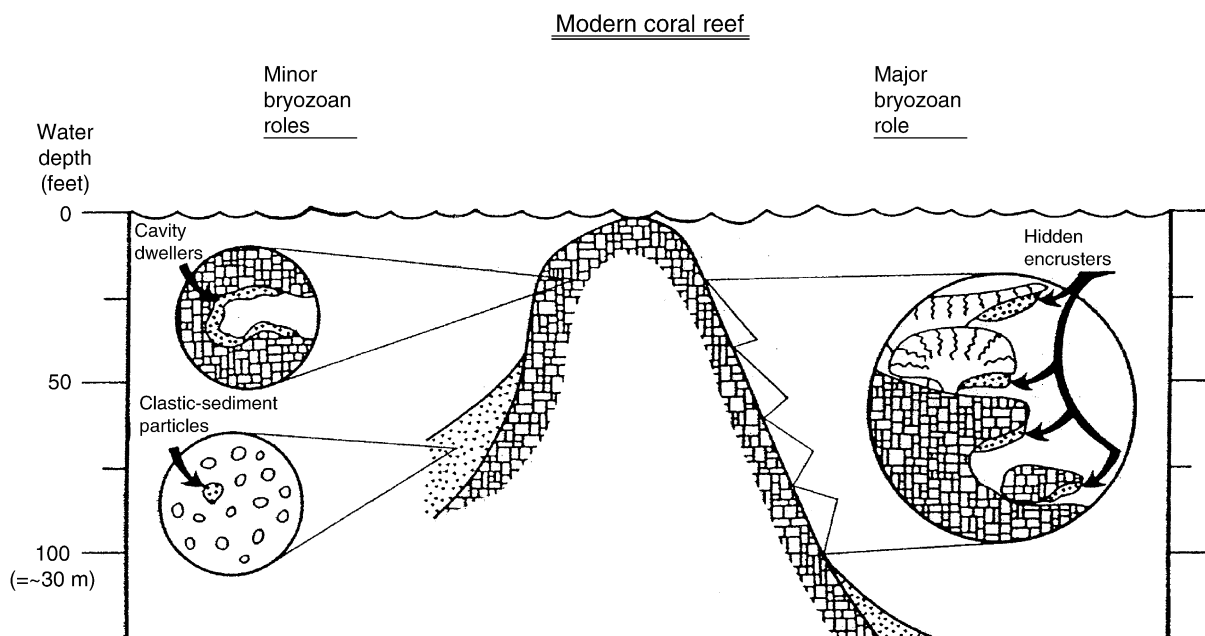
### Roles seen among reefal bryozoans

The manner in which bryozoans occur on modern reefs has obvious implications about how their calcareous skeletons might contribute to reef building or reef communities, the *constructional or ecologic roles* played by these animals. These roles were initially defined for modern



**Bryozoa, Figure 1** Reefal bryozoan groups, identifiable by their distinctive colony shapes (*zoarial forms*); aeteids and reteporids are also cheilostomes, while crisiids, idmoneids, and lichenoporids are cyclostomes. From Cuffey (1973, p. 30).





**Bryozoa, Figure 2** Roles played by bryozoans in modern coral reefs. After Cuffey (1972, p. 547).

coral reefs (Figure 2; Cuffey, 1972) and later expanded to cover both living and fossil reefs (Cuffey, 1977).

Most of the bryozoans encountered on modern coral reefs are *hidden encrusters* (Cuffey, 1972), their colonies attached to the undersides (Figure 3) of coral branches, fronds, or heads, and of reef-rock fragments, rubble, or ledges, as well as of shells or other hard substrates (both natural and artificial). Equivalent terms used later for this principal reefal-bryozoan role include *coelobites*, *coelobionts*, *cryptobionts*, and *cryptic fauna*; hidden encrusters comprise the bulk of the wider category of *accessory frame encrusters* (Cuffey, 1977). During life, such bryozoan colonies compete for attachment space with other sessile organisms – serpulids, certain pelecypods and gastropods, sponges, encrusting foraminiferans, and various calcareous algae like lithothamnioid *corallines*.

In addition to the sheltered undersides of the coral framework, there are deeper, darker niches, recesses, and cavities within modern reefs. These may also contain bryozoan crusts, ranging from thin and unilaminar to thicker and multi-layered, locally even filling those spaces. Such bryozoans can be described as *cavity dwellers* or even *cavity fillers* (Cuffey, 1972, 1977); their calcareous encrustations can contribute to reinforcing or strengthening the overall reef framework.

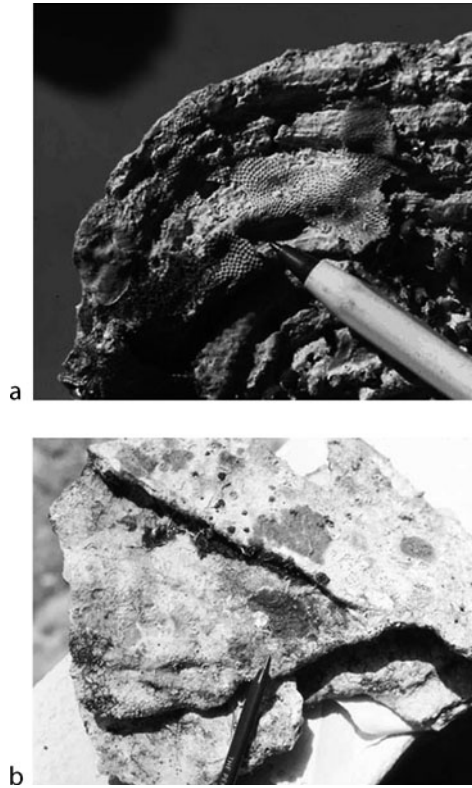
Modern reefs include very few actually built by bryozoans themselves. However, three are now known – *Bahamas* (Joulter Cays tidal channel, Cuffey et al., 1977), *Netherlands* (coastal ponds, Bijma and Boekschoten, 1985), and *Australia* (Coorong Lagoon; Bone and Wass, 1990) – all quite small, of limited diversity, and in ecologically marginal habitats compared with flourishing coral reefs.

In contrast, at several phases in the geologic past, different bryozoan taxa constructed reefs or *Bioherms* and *Biostromes* of various sizes (Cuffey, 1977, 1985, 2006).

Bryozoans might be expected to be important sediment formers on and around modern coral reefs, since their colonies are common on many such structures. Surprisingly, however, examination of loose sediments surrounding living reefs reveals only occasional small fragments of broken bryozoans (Cuffey, 1972). Clearly, cheilostome crusts' microstructure proves to be comparatively weak and quickly destroyed when eroded off the reefs. In contrast, some fossil reefs are surrounded by clastic carbonates composed entirely of bryozoan detritus (Pitcher, 1964; Cuffey, 1977).

Bryozoan-rich sands do cover parts of the present-day continental shelves around Australia, including some of the individual reefs within the *Great Barrier Reef: Origin, Evolution, and Modern Development* complex (Maxwell, 1968, p. 190, 205–208). However, their colony forms and presumed species identities do not match those observed on the actual reefs (Cuffey, 1978), so these bryozoans do not appear to be strictly reefal in the sense talked about throughout this article, but probably inhabited deeper bottoms between the individual reefs. This suspicion is reinforced by the discovery of extensive similar bryozoans-rich sands extending south into clearly non-reef regions (Wass et al., 1970).

Various other minor roles have been noted for bryozoans, some in modern reefs, but most in ancient fossil *Bioherms* and *Biostromes* (Cuffey, 1972, 1977, 2006). One species seen in Bermuda, the Bahamas, and Florida, *Membranipora* or *Jellyella tuberculata*, encrusts



**Bryozoa, Figure 3** Typical field appearance of reefal bryozoans (hidden encrusters; pen-points for scales); (a) underside of Bermuda brain coral (*Diploria*) encrusted (center) by cheilostome *Steginoporella magnilabris*; (b) undersides of Bonaire flat cobbles (broken *Millepora* blades), bearing several small round cheilostome crusts (the one closest to pen-point is *Trematoecia turrita*).

*Sargassum* brown algae drifting through surface waters around the reefs and so is often found washed up on nearby beaches. In older fossil reefs, branching and lattice bryozoans inhibited movement of loose sediments around reefs, functioning as *sediment baffles*, *trappers*, *binders*, or *stabilizers*. In other reef structures, dead coral bioherms' surfaces were covered by a solid veneer of encrusting bryozoans. In still others, originally more extensive bryozoan crusts appear so corroded and partially dissolved that they obviously served as a source of dissolvable carbonate during diagenesis.

### Continuing investigations

After elucidation of the reefal bryozoans' roles, investigations of these animals have continued, diversifying into several different types of studies.

Most immediate have been documenting species identities and distributions within various living reefs like *Bermuda* (Cuffey and Fonda, 1986), *Enewetak Atoll, Marshall Islands* (Cuffey and Cox, 1987), *Belize* (Winston, 1984), *Bali* and other *Indonesian Reefs*

(Winston and Heimberg, 1986), the *Solomons* (Tilbrook, 2006), and others.

In addition to these faunal studies, others have focused on particular reefal-bryozoan species' ecology (Cuffey and Foerster, 1975; Cuffey and McKinney, 1982) and interactions like competitive overgrowths (Jackson, 1979). A few new species have been reported from certain remote reefs like *Enewetak Atoll, Marshall Islands* (Cuffey and Cox, 1987); otherwise, known reefal species do not appear to be restricted exclusively to reef habitats. Within-species variability, particularly in colony form, can in certain species be related to wave energy; *Schizoporella errata* in *Bermuda* grows into compact nodular masses under turbulent conditions, but erect open branches in quiet situations (Cuffey and Fonda, 1976).

Modern coral reefs exhibit *Geomorphic Zonation*, the best example of which is the *Atlantic/Caribbean Forereef/Reef Front* corals (shallow *Acropora palmata*, middle *Acropora cervicornis*, and deep *Montastrea annularis*). Reefal bryozoans however, do not show such depth-related species assemblages; instead, the various species' depth ranges overlap progressively and gradually, going down the *reef front (Forereef/Reef Front)*, as documented on Bonaire's reef-slope (Kobluk et al., 1988). The particular individual species' depth ranges may prove useful in paleoecologic interpretations, however, even if multispecies assemblages can not be recognized. Moreover, depending on the number and abundances of the shallowest species, a diver in the field may observe that some reefs have abundant bryozoans from the sea-surface on down, whereas others show common colonies only below 10 m or 30 ft (like *Bermuda* and *Enewetak Atoll, Marshall Islands* respectively; Cuffey, 1973).

In contrast to vertical or depth *Geomorphic Zonation*, reefal bryozoans in some cases show horizontal *Geomorphic Zonation*, related to distance from shore or open ocean. Reefal (i.e., off-shore) versus in-shore species suites can be recognized in *Bermuda* (Fonda and Cuffey, 1976), as can diversified outer-reef versus restricted lagoonal-reef assemblages in the *Bahamas* (Cuffey and Fonda, 1977).

Traditionally, reefal bryozoan species have been identified by examining their colonies' horizontal upper surfaces. However, those surfaces are often covered, not visible, when reef masses are cut into by quarrying, road-cuts, or ship groundings, and hence their bryozoans' appearance in vertical cross-sections must be used instead for identifications to determine the particular species involved in those reefs. Taxonomists have not usually published such views, and thus work has begun on coordinating surface with cross-section appearances (Kosich and Cuffey, 1978). Preliminary results have been used successfully on modern bryozoan reef rock at Joulter's Cays (Cuffey et al., 1977).

A great many other aspects of bryozoan involvement in modern and geologically recent fossil reefs could be analyzed – physiologic, biogeographic, pharmaceutical, geochemical, etc. However, not enough time nor workers

have yet become involved with reefal bryozoans for such greater scientific diversification to have developed so far. Much remains to be done!

## Summary

Although initially overlooked by reef scientists, bryozoans living on or in modern coral reefs are common and diversified on many such structures, particularly in their principal role as hidden encrusters. Much detailed work needs to be done yet to fully elaborate many aspects of reefal bryozoan taxonomy, distribution, and ecology.

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## Cross-references

[Acropora](#)  
[Algae, Coralline](#)  
[Atolls](#)  
[Bahamas](#)  
[Belize Barrier and Atoll Reefs](#)  
[Bermuda](#)  
[Bioherms and Biostromes](#)  
[Coral Reef, Definition](#)  
[Enewetak Atoll, Marshall Islands](#)  
[Florida Keys](#)  
[Forereef/Reef Front](#)  
[Geomorphic Zonation](#)  
[Great Barrier Reef: Origin, Evolution, and Modern Development](#)  
[Indonesian Reefs](#)  
[Makatea](#)  
[Pacific Coral Reefs: An Introduction](#)  
[Platforms \(Cemented\)](#)  
[Western Atlantic/Caribbean, Coral Reefs](#)

# C

## CALCITE

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### Definition

The minerals calcite, *aragonite*, and *vaterite* are naturally occurring polymorphic forms of calcium carbonate ( $\text{CaCO}_3$ ). At normal Earth surface pressures and temperatures, low magnesian calcites are the only stable  $\text{CaCO}_3$  phase. Calcite has a trigonal crystal system, perfect cleavage in three directions, conchoidal fracture, and a hardness of three on Moh's scale. Calcite often has a massive habit, although dog-tooth spar (scalenohedrons) and rhombohedral forms are also common. The mineral's color is commonly white or colorless, but may be yellow, pink, pale blue, or even red in hand specimen; in thin section, it is colorless. Most calcite is relatively pure, but impurities include ferrous iron, magnesium, manganese, and strontium. Calcites with less than four mole percent  $\text{MgCO}_3$  are termed low magnesian calcites, while those containing 4–30 mole percent are known as high magnesian calcites. Calcite is readily soluble and effervesces vigorously in cold dilute hydrochloric acid and it is stained red by the organic dye Alizarin Red S.

Calcite is generally a major constituent of carbonate rocks and is a commonly found earth mineral. Limestones must be made of more than 50% carbonate minerals (Tucker and Wright, 1990). Calcite tends to precipitate from freshwater where Mg:Ca ratios are generally low (<1). Carbonate minerals are highly soluble in waters rich in carbon dioxide, which results in most limestones being susceptible to *diagenesis*. *Diagenesis* leads to the alteration of a carbonate deposit by various geochemical processes that result in changes in mineralogy, texture, and fabric.

Over time, skeletal and non-skeletal carbonate grains and carbonate matrix alter to low magnesian calcite and calcite cements are precipitated in primary and secondary pore spaces. In the process, *aragonite* is often partially or totally dissolved. During transformation from high to low magnesian calcite, the initial structure is kept but  $\text{Mg}^{2+}$  is leached from the crystal. The crystal sizes of calcite cements that form can be grouped into *micrite* (<4 microns), *microspar* (4–10 microns), and *spar* (>10 microns).

Typical freshwater low magnesian calcite-rich deposits include *calcretes*, tufa, travertine, cave speleothems, and *eolianites*. High magnesian calcites are common components of *beach rocks*, shallow marine sediments, and the skeletons of marine organisms. According to Mackenzie et al. (1983), there is an increase in the content of magnesium within skeletal high magnesian calcite from polar regions towards the tropics, which is related to changes in temperature and seawater saturation of carbonate ions.

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### Cross-references

[Aragonite](#)  
[Beach Rock](#)  
[Calcrete/Caliche](#)  
[Diagenesis](#)  
[Eolianite](#)  
[Micrite](#)

## CALCRETE/CALICHE

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### Synonyms

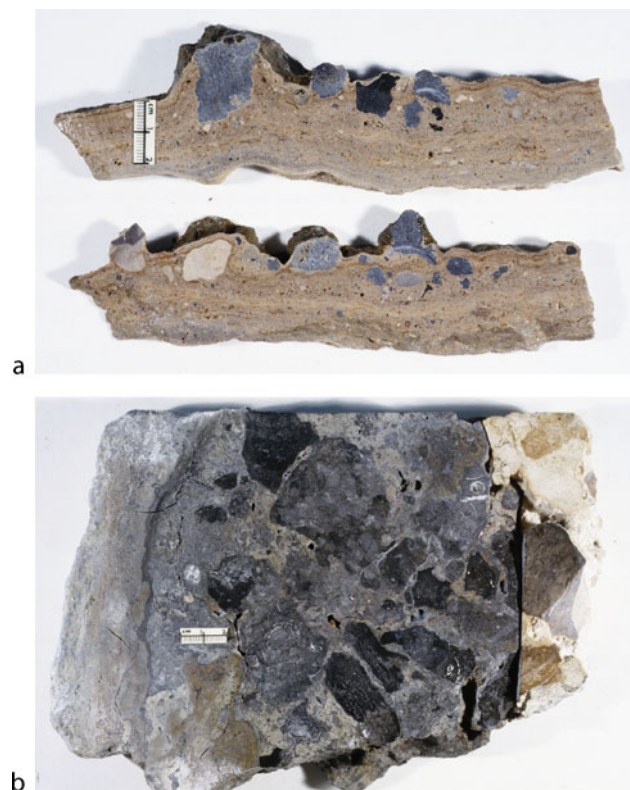
Breccias; Calcium-carbonate cement; Hardpan; Impermeable crust of soluble calcium salts; Laminated crust; Pedogenic calcareous soil; Secondarily deposited calcareous material on native-limestone surface; Soilstone crust; Strongly indurated wafer-thin calcareous layers; Subaerial  $\text{CaCO}_3$  crust; Subaerial-exposure surface; Unconformity

### Definition

Laminated subaerial-soilstone crusts (calcrete/caliche) are found in diverse carbonate environments throughout geological history (e.g., Swett, 1974; Harrison and Steinen, 1978; Kahle, 1978). Florida crusts accrete vertically in a series of wafer-thin layers, through capillary interaction of wet/dry processes on exposed limestone (Multer and Hoffmeister, 1968). The limestone underlies a thin mantle of organic-rich soil that contains cryptocrystalline calcite, derived from periodic dissolution of in situ carbonate particles. Drill cores show Florida crusts cap five Pleistocene chronostratigraphic marine sequences, as unconformities (Enos and Perkins, 1977). Extensive subsurface persistence renders the crusts significant stratigraphic markers for regional sequence correlation. Radiometric dates that correlate with Pleistocene glacial cycles indicate times when subsurface crust-source sites were dry land (Robbin, 1981). In the Florida Keys, crust accretion rates are uniform within, but inconsistent between, northeast (1 cm/2 ka) and southwest (1 cm/4 ka) sites (Robbin and Stipp, 1979). Inconsistency results from different local ambient conditions during crust formation (e.g., variability of limestone porosity, soil, humus, detrital carbonate, and erosion). Inconsistent accretion rates result in different thicknesses of calcrete (see Figure 1a and b in entry entitled, *Porosity Variability in Limestone Sequences*).

### Calcrete textures

Calcretes have various textures depending upon the type of material present at the site of formation and/or the processes involved in formation. Rhizoliths or rhizoconcretions are small cylindrical or conical root-cast structures, usually branching or forked, that form in a sedimentary rock. Rhizoliths may consist of calcrete or chert and resemble in shape the plant roots they have replaced. Calcretes that consist of aggregated, clustered, or flocculated grains are said to be clotted. Patches of dark, dense, fine-grained areas ultimately surrounded by sparry calcite can characterize clotted rocks. The squashing of soft micrite pellets usually produces clotting. Calcretes that have different colors, commonly resulting from oxidation of iron components, are said to be mottled, but



**Calcrete/Caliche, Figure 1** (a) Large, angular, naturally blackened pebbles embedded in brown, layered, fine-grained calcrete form a breccia (compare with calcretes shown in a and b in entry entitled, *Porosity Variability in Limestone Sequences*). Sample is from Ramrod Key (lower Florida Keys). Ramrod Key limestones also contain charred twigs (charcoal; not shown). Charcoal in 5-ka calcrete indicates natural forest fires occurred before the invasion of modern man. (b) A multicore breccia was collected at a depth of ~6 m below sea level from quarry tailings in a solution pit on Big Pine Key (lower Florida Keys). The sample was cut, and the left part artificially blackened in the laboratory by heating at 400°C for one-half hour to reproduce darkening similar to colors of blackened pebbles widely found in the Florida-Caribbean Pleistocene and Holocene record. Note layered calcrete crust on left side of specimen. Blackened fragments include preexisting calcrete and fossiliferous Key Largo Limestone (coral). Original rock colors are visible in unheated section at right. Rulers in both photos are 2 cm long. See Figure 2a in entry entitled, *Florida Keys*, for locations of Ramrod Key and Big Pine Key.

multicoloration is not the only characteristic. Mottled calcretes also can contain small irregular pieces of material in a sedimentary matrix of a different texture.

Breccias are coarse-grained clastic rocks composed of angular fragments of any kind of preexisting native rock. Mineral cement binds the fragments together in a fine-grained matrix of sand, clay, or calcrete. Breccias may result from talus accumulation (sedimentary breccia), igneous processes (volcanic and explosive breccias), tectonic processes (fault breccia), disturbance during



sedimentation (intraclastic breccia), or collapse of rock material (solution and collapse breccias). Solution and collapse breccias are common in karst settings such as Florida where sinkholes and other types of karst features form. Also common in Pleistocene and Holocene limestones throughout the Florida-Caribbean region are multihued blackened limestone pebbles in a calcrete matrix (Figure 1a and b). Simple laboratory (heating) experiments and observations (campfire sites) have shown that pebbles of limestone (coral, mollusc, grainstone, and calcrete) can blacken almost instantaneously when heated to between 400° and 500°C (Shinn and Lidz, 1988). Being the lightning capital of the U.S., Florida has, and has had in the geological past, no shortage of sources of ignition for lighting of natural forest fires.

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## Cross-references

[Florida Keys](#)  
[Last Glacial Lowstand and Shelf Exposure](#)  
[Porosity Variability In Limestone Sequences](#)  
[Reef Drilling](#)

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## CARBON FLUXES OF CORAL REEFS

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## Synonyms

Carbon dynamics

## Definition

The carbon fluxes of coral reefs are the rates of carbon exchange between sea water and reef organisms, communities, and habitats. They characterize key biochemical processes such as photosynthesis, respiration, and calcification, as well as important biogeochemical transformations such as diagenesis and dissolution. Fluxes are reported as rates of exchange per area.

## Introduction

A coral reef is a living structure that maintains itself at sea level by the combined biogenic calcification of a variety of taxa. A healthy, sustainable coral reef ecosystem is comprised of diverse communities that capture and utilize energy from sunlight, waves, and organic particles. The motivation for studying carbon fluxes of coral reefs is to delineate and characterize these rates of energy transfer in order to compare reefs with other ecosystems and to compare among reefs, and to predict responses of reefs to natural or anthropogenic perturbations.

Specific communities within a coral reef ecosystem achieve high rates of photosynthesis and, consequently, production of organic carbon. Over the past 80 years, a variety of ideas have been advanced to explain these high rates of carbon production. One prevalent view is that close physical and ecological relationships between autotrophs (organisms such as plants that produce organic carbon from inorganic carbon) and heterotrophs (organisms that consume organic carbon, i.e., most animals) create an ecosystem where plant nutrients (compounds of nitrogen, phosphorus, sulfur, etc.) are either retained within the biota or recycled within the community, maximizing carbon production. A more recent view is that coral reefs produce organic carbon that is low in nutrients and is quickly respired. This article provides an overview of the carbon dynamics or carbon fluxes of coral reefs.

## Fluxes of dissolved inorganic carbon

The amount of carbon, in both dissolved and particulate forms, is orders of magnitude lower in the water column above a coral reef than it is in the biota or in the sediments (Table 1). Dissolved inorganic carbon (in the form of dissolved carbon dioxide and carbonate and bi-carbonate ions) is removed from the water column by autotrophs and converted to, or “fixed” into, both organic compounds (tissue and dissolved organic compounds) and inorganic compounds (notably calcium carbonate skeletons of marine algae and corals; Kinsey, 1985; Hatcher, 1997; Gattuso et al., 1998; Atkinson and Falter, 2003). The total amount of carbon fixed into organic matter per day is termed gross primary production. Gross primary production is typically estimated by adding daytime net photosynthesis to the 24-h respiration rate, based on dark respiration. Light respiration can be up to two times greater than dark respiration. Published values of gross primary production that assume light respiration equals dark respiration are therefore of questionable accuracy

(Langdon et al., 2003). In practice, flux of oxygen is used instead of carbon dioxide to estimate net photosynthesis and respiration, assuming photosynthetic and respiratory quotients of 1.0 (range 0.8–1.2). Many such measurements have produced a uniform “metabolic standard” for reefs (Table 2).

Gross primary production varies from 100 to 2,000 mmol C m<sup>-2</sup> d<sup>-1</sup>, depending on habitat (Table 2). Sand communities have the lowest production (100–300 mmol C m<sup>-2</sup> d<sup>-1</sup>), with reef flats being moderate (350–500 mmol C m<sup>-2</sup> d<sup>-1</sup>), and communities with high surface area of coral and algae exhibiting maximal values (1,000–2,000 mmol C m<sup>-2</sup> d<sup>-1</sup>). These metabolic rates are consistent between reefs, suggesting that they are independent of species composition. Thus, carbon metabolism on reefs has a tri-modal distribution (Table 2), and estimates of carbon production and calcification (production of calcium carbonate) can be made based on knowledge of bottom type or habitat. These three basic habitats of

coral reefs can be easily identified and mapped with airborne and satellite imaging systems (Hochberg et al., 2003). Ecosystem-wide estimates of gross primary production are possible by applying average metabolic rates to the areal extent of those habitats (Andrefouet and Payri, 2000). Gross primary production can also be estimated by measuring the number of photons absorbed into the benthos with remote-sensing image data and multiplying by 0.033 mol oxygen/mol photons (Hochberg and Atkinson, 2008). Thus, the amount of energy converted from tropical sunlight to organic matter on a reef flat represents about 3% efficiency. Sunlight incident on tropical reef flats is typically ~30–40 Einstein m<sup>-2</sup> d<sup>-1</sup> or 10,000 kJ m<sup>-2</sup> d<sup>-1</sup>, whereas 1 mol organic C m<sup>-2</sup> is about 400 kJ m<sup>-2</sup>.

Community respiration varies over the same range as gross primary production (Table 2). Benthic communities with high gross primary production tend to exhibit high community respiration, indicating much of the respiration of organic material occurs within the habitat. Most of the respiration probably occurs within the organisms that fix the carbon; some is the result of consumption and/or microbial decomposition of organic detritus. Measurements of production and respiration over periods shorter than 1 week do not adequately reflect longer-term net ecosystem metabolism. This is because in the case of autotrophs, a day's gross primary production depends on cumulative ambient light on that day; the daily gross respiration depends on the amount of stored photosynthate on that day (Falter et al., 2001).

### Net production of carbon

Net community production (NCP – Table 2), the excess carbon produced over a 24-h period (gross primary production minus community respiration), varies among habitats. In classic reef zonation, more carbon is produced than is respired on the fore-reef and algal crest, instead being exported to the back-reef area as detritus and dissolved organic carbon. As it is carried across the reef, a proportion of it is utilized by downstream heterotrophic communities (Crossland et al., 1991; Kinsey, 1985). In practice, the delineation between producer and consumer habitats is not always clear. For example, many back reef

**Carbon Fluxes of Coral Reefs, Table 1** Mass of carbon (C) in mmol m<sup>-2</sup> in 1 m of the water column above the benthos, in the living benthos (autotrophic and heterotrophic), and in the top-most 1-m of sediments (solid and dissolved phases)

| Pool             | C                    |
|------------------|----------------------|
| 1-m water column | 10–250               |
| Living benthos   |                      |
| Autotrophic      | 22,400 <sup>a</sup>  |
| Heterotrophic    | ~5,000 <sup>b</sup>  |
| 1-m sediments    |                      |
| Solid phase      | 300,000 <sup>c</sup> |
| Dissolved phase  | 5–125 <sup>d</sup>   |

<sup>a</sup>Values for benthic autotrophs calculated from dry weight biomass estimates (Odum and Odum, 1955) and assuming a C:N:P ratio of 550:30:1 (Atkinson and Smith, 1983).

<sup>b</sup>Benthic heterotrophic biomass content calculated assuming nearly all of the biomass is composed of CH<sub>2</sub>O

<sup>c</sup>Assuming a porosity of 0.5 (Buddemeier and Oberdorfer, 1988) and a sediment density of 2.7 g cm<sup>-3</sup>.

<sup>d</sup>This estimate assumes pore water dissolved organic carbon concentrations are equal to ambient water dissolved organic carbon concentrations (Tribble et al., 1990).

**Carbon Fluxes of Coral Reefs, Table 2** Gross primary production (P), Community respiration (R), Net Community Production (NCP), and Net Community Calcification (G) in mmol C m<sup>-2</sup> day<sup>-1</sup> for various habitats as originally tabulated by Kinsey (1985) with additional data from Gattuso et al. (1993), Gattuso et al. (1996), Kraines et al. (1996), Kraines et al. (1997), Boucher et al. (1998), and Andrefouet and Payri (2000). Means are in **bold** followed by the range in parentheses. To convert to grams of carbon, multiply by 12 g mol<sup>-1</sup> and divide by 1,000 mg g<sup>-1</sup>. A negative value for NCP indicates that habitat must import organic carbon to match its respiratory demand

| Habitat             | P                        | R                        | NCP      | G                    |
|---------------------|--------------------------|--------------------------|----------|----------------------|
| Average reef-flat   | <b>640</b> (330–1,580)   | <b>600</b> (290–1,250)   | –220–310 | <b>130</b> (20–250)  |
| Algal pavement      | <b>460</b> (170–580)     | <b>300</b> (40–560)      | 0–130    | <b>90</b> (70–110)   |
| High coverage       | <b>1,180</b> (660–1,920) | <b>1,280</b> (500–2,000) | –830–250 | <b>240</b> (110–320) |
| Sandy areas         | <b>130</b> (80–230)      | <b>130</b> (90–200)      | –40–30   | <b>35</b> (10–70)    |
| Shallow lagoon      | <b>450</b> (210–1,080)   | <b>430</b> (180–790)     | –200–280 | <b>40</b> (20–55)    |
| Entire reef systems | <b>390</b> (190–640)     | <b>370</b> (190–570)     | 0–70     | <b>45</b> (3–135)    |

areas that have significant coral rubble can have high net production. Thus, much of this zonation of production and consumption is dependent on the nature of the substrate. Sand and mud have a tendency to be heterotrophic (negative net production), while areas exposed to high water motion and hard substratum with algae tend to be autotrophic (positive net production). Rich coral areas and knolls usually have high gross production, but a net production that is close to zero. Seaward areas with a relatively high net production can be sustained by dissolved nutrients in the incoming ocean waters, and where high water motion can support higher nutrient uptake and photosynthetic rates than calmer areas (Hearn et al., 2001; Carpenter and Williams, 2007). Nutrient uptake is proportional to nutrient concentration and water velocity, with a coefficient of proportionality that is directly related to the friction of the water flowing over the bottom communities (Atkinson and Falter, 2003). The energy dissipated as bottom friction helps drive net photosynthesis and net production of carbon, and is of order  $1,000 \text{ kJ m}^{-2} \text{ d}^{-1}$  (Hearn et al., 2001), or about 10% of the energy in sunlight for typical cross-reef currents. Organic carbon production has high ratios of carbon:nitrogen:phosphorus (C:N:P), reflecting dominant production by macrophytes (Atkinson and Grigg, 1984).

### Fluxes of planktonic carbon

Coral reef communities take up suspended planktonic organic matter (detritus, phytoplankton, zooplankton) as a source of “new” carbon – i.e., carbon they do not fix themselves via photosynthesis (Ayukai, 1995; Ribes et al., 2003; Yahel et al., 1998). Reported rates of particulate carbon uptake are, however, relatively low ( $<40 \text{ mmol C m}^{-2} \text{ day}^{-1}$ ), compared to rates of gross primary production and community respiration (Table 2). Suspended organic matter is thus relatively unimportant as a source of carbon for many hard and soft coral communities. However, it is an important source of specific essential nutrients for many communities, and food for some (Fabricius et al., 1998; Sebens et al., 1997).

### Fluxes of dissolved organic matter

Dissolved organic carbon comes from microbial decomposition of plant and animal detritus and fecal material. It is ubiquitous in water over coral reefs, and it typically occurs at concentrations much greater than those of particulate organic matter ( $50 \text{ mmol m}^{-3}$ ). Dissolved organic carbon is taken up and released by a variety of organisms, including corals and sponges (Schlichter and Liebezeit, 1991; Hoegh-Guldberg and Williamson, 1999; Yahel et al., 2003). Rates of dissolved organic matter metabolism can be either significant or insignificant in the context of total metabolism. Much of the metabolism has been attributed to symbiotic bacteria (Ferrier-Pages et al., 1998; Yahel et al., 2003), but the cycling of dissolved organic matter at the community and ecosystem scales remains poorly understood. The metabolism of specific organic

compounds occurring in low concentrations, such as steroids, can have substantial impacts on the biology of specific organisms (Tarrant et al., 2004).

Reef waters also contain dissolved organic nitrogen; it is typically exported from reef communities (Wilkinson et al., 1984). The nature of dissolved organic nitrogen and the rate kinetics of its uptake are also unknown, making it difficult to establish their rates of uptake or recycling. Like dissolved organic compounds, generally, dissolved organic nitrogen may be resistant to chemical breakdown in seawater and require bacterial or sponge communities for re-mineralization; its uptake and release by the benthic community will thus strongly depend on the composition and abundance of the benthic biota.

### Fluxes of sediment carbon

Sediments in coral reefs typically contain  $<1\%$  organic carbon, indicating little sequestration of organic carbon into these systems. By contrast, rates of inorganic carbon deposition (as calcium carbonate skeletons) are large, its production accounting for approximately 10–20% of gross primary production. Communities with high gross primary production tend to have the highest calcification rates (Table 2). Calcification is positively correlated to light and net photosynthesis (Gattuso et al., 1999); the activation energy to produce a typical amount of calcium carbonate represents only 1% of the energy in gross primary production (activation energy for carbonate precipitation is  $\sim 4 \text{ kJoule m}^{-2} \text{ d}^{-1}$  for  $0.1 \text{ mol CaCO}_3 \text{ m}^{-2} \text{ d}^{-1}$ ). The rate of calcification is positively correlated to carbonate ion concentration in the sea water (Atkinson and Cuet, 2009); projected decreases in carbonate over the next 60 years from rising atmospheric carbon dioxide may reduce coral calcification by up to 30% (Smith and Buddemeier, 1992; Kleypas and Langdon, 2006). Dissolution of carbonates occurs naturally inside coral heads (Entsch et al., 1983), in interior pore-spaces of coral reef sediments (Tribble et al., 1990), and from the erosion action of boring organisms (Tribollet, 2008). Historically, rates of dissolution have been much slower than rates of biogenic precipitation ( $<10\%$ ; Tribble et al., 1990), but it is now suggested (Hoegh-Guldberg et al., 2007) that ocean acidification will reverse the relative rates.

### Pore-water carbon

Coral reef frameworks are partially lithified carbonate structures on which reef communities grow. Pore-waters of reef frameworks are mostly anoxic and contain elevated levels of dissolved nutrients (Sansone et al., 1990). This combination of low oxygen and high nutrients is a common feature of many coral reefs and a direct result of oxidation of organic matter in the interstitial spaces (Tribble et al., 1990). The subsequent production of carbonic acid from the oxidation of organic matter lowers pore-water pH and reduces the activity of the carbonate ion, thus facilitating *in situ* dissolution of carbonate (primarily aragonite). Reef pore-waters become anoxic at



depths of less than 1 m into the framework; however, some reef pore waters become anoxic within centimeters of the framework surface (Falter and Sansone, 2000b).

Hydraulically driven transport of water into, through, and out-of coral reef frameworks has long been hypothesized as the primary driver of framework diagenesis – the transformation of skeletal materials into limestone rock (Haberstroh and Sansone, 1999). It is proposed that the water brings both oxygen and particulate organic matter into the interstitial pore-spaces to sustain carbon metabolism (Huettel and Rusch, 2000). Coral reef frameworks are highly permeable, typically with hydraulic conductivities (K) ranging between 10 and 1,000 m day<sup>-1</sup>. Consequently, ambient hydraulic pressure gradients across coral reef frameworks do seem large enough to drive the flow of interstitial water (Falter and Sansone, 2000a) and thus drive diagenesis in the manner postulated. Wave-induced mixing is an important process controlling the exchange of shallow pore-water with overlying water (Falter and Sansone, 2000a). Thus, variations in the oxygen and pH structure of pore-waters within the top 2 m of sediment are affected by a habitat hydrodynamics, which is affected by its location on the reef and the direction of waves impinging on the reef. The deep anoxic regions of the reef frameworks, beyond the effects of wave-induced mixing, are high in methane and sulfate (Sansone et al., 1990).

## Summary

Ranges, means, and limits of carbon metabolism are summarized for coral reefs worldwide; zones and habitats of carbon production and consumption are also described. The underlying functional processes and parameterizations of those processes are discussed. At this time, however, there are gaps in knowledge, and it is particularly noted that interactions with nutrients are not yet well established.

Dissolved inorganic carbon (i.e., carbon dioxide gas, bicarbonate, and carbonate ion) is removed from the water column by autotrophs and fixed into organic (tissue and photosynthate) and inorganic (calcium carbonate skeletons) compounds. Gross primary production and community respiration rates vary greatly in different habitats of reefs, with much of the respiration of organic material occurring within the organism or the habitat in which it was produced. Net community production varies among habitats. In classic reef zonation, carbon from the fore-reef is exported to the back-reef area as detritus and dissolved organic carbon. Coral reef communities take up suspended planktonic organic matter at rates that are relatively low compared to their own primary production. Sediments in coral reefs typically contain <1% organic carbon, indicating little sequestration of organic carbon into these systems. Dissolution of calcium carbonate occurs naturally inside coral heads, in interior pore-spaces of coral reef sediments, and from the erosion action of boring organisms. Globally, the surface area of coral reefs is

small and thus coral reefs have negligible effect on the global carbon cycle.

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## Cross-references

[Carbonate Budgets and Reef Framework Accumulation](#)  
[Diagenesis](#)  
[Dolomitization](#)  
[Nutrient Pollution/Eutrophication](#)  
[Ocean Acidification, Effects on Calcification](#)  
[Platforms \(Cemented\)](#)  
[Solution Processes/Reef Erosion](#)

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## CARBONATE BUDGETS AND REEF FRAMEWORK ACCUMULATION

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### Definition

Carbonate budget: A quantitative measure, typically using census-based data, of the net rate of carbonate production within a given reef or carbonate sedimentary environment. The approach enables rates of reef carbonate production and erosion, associated with different biological, chemical and physical processes, to be quantified.

### Introduction

In many tropical reef environments, corals are important primary producers of calcium carbonate (CaCO<sub>3</sub>) and thus play a key role in reef framework construction. High percentage coral cover is often taken as indicative of a high rate of CaCO<sub>3</sub> accumulation and thus of rapid reef growth potential. However, corals represent just one of the carbonate producing groups that contribute to reef

construction. Carbonate is also added to a reef's structure by calcareous algae and other calcareous encrusting organisms, through carbonate sedimentation, and by the precipitation of marine cements. Alongside these constructive processes, a range of physical and biological processes also operate to directly erode the accumulating reef structure. This eroded carbonate may subsequently re-accumulate within the reef structure or be exported out of the reef system. Summing the rates at which these different carbonate producing and eroding processes operate, thus allows the net rate of carbonate production on a reef to be quantified. A carbonate budget is thus a summation of the inputs and outputs of carbonate within the active carbonate producing environment and is typically expressed as a measure in  $\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ . Carbonate budget assessments, although logistically complex to construct, thus provide a useful estimation of net carbonate production rates on a reef at a given point in time. They also provide a mechanism for quantifying the relative importance of different carbonate producing and eroding processes, and provide an important insight into inter-reef variations in styles and rates of reef framework development. This has relevance to understanding both variability in the composition of accumulating reef framework structures and actual rates of framework accumulation.

### Quantifying reef framework production and cycling

Coral reefs and reef sedimentary landforms are unique in that they are composed predominantly of calcium carbonate ( $\text{CaCO}_3$ ) that results almost entirely from ecological processes. Corals typically represent the primary constructional components on most reefs and can add significant amounts of carbonate per unit area of reef surface (Vecsei, 2004). However, other carbonate producing processes also add additional  $\text{CaCO}_3$  to the reef framework, the most important being by calcareous encrusters (especially crustose coralline algae), and the precipitation of syn- and early post-depositional cements (Perry and Hepburn, 2008). Significant amounts of primary carbonate are also produced in the form of sediment by other organisms or plants that induce  $\text{CaCO}_3$  deposition. These additional sources of carbonate can contribute significant quantities of carbonate to the reef structure and may actually dominate  $\text{CaCO}_3$  accumulation in specific reef settings (Bosence, 1984; Camoin et al., 2006).

A range of physical and biological erosional processes also influence rates and styles of reef framework accumulation. Bioerosion (the biological erosion of carbonate substrates) is facilitated by a wide range of reef-associated faunas, including species of fish and echinoids, and endolithic forms of sponges, bivalves and worms (see Chapter *Bioerosion*). These biological agents drive the direct degradation of both primary and secondary reef framework constituents and, as a by-product, may produce large amounts of sediment (Scoffin et al., 1980; Bruggemann et al., 1996). Physical disturbance, associated with storms and cyclones, is an important episodic process that influences reef framework development, largely

through the generation of coral rubble, the deposition of which is an important reef-building process in its own right (Hubbard, 1997; Blanchon et al., 1997), and through the export of reef-derived sediments (Hubbard et al., 1990).

These various carbonate producing and cycling processes may thus exert either a "constructive" or "destructive" (*sensu* Scoffin, 1992) influence on reef-related carbonate accumulation, and the relative importance of each, within a given reef system, controls net rates of carbonate accumulation. This concept is defined by the carbonate budget approach to conceptualizing and quantifying reef geomorphic performance and can be viewed as the sum of gross carbonate production from corals and calcareous encrusters, as well as sediment produced within or imported into the reef, less that lost through biological or physical erosion, dissolution or sediment export (Figure 1). The balance between these different inputs and outputs represents the net production rate of framework  $\text{CaCO}_3$  and can be expressed as:

$$\text{Net rate of framework CaCO}_3 \text{ production} = [(P_{\text{pf}} + P_{\text{sf}}) - P_{\text{e}}] + \text{Sed}_i$$

where

$P_{\text{pf}}$  = Primary framework carbonate production.

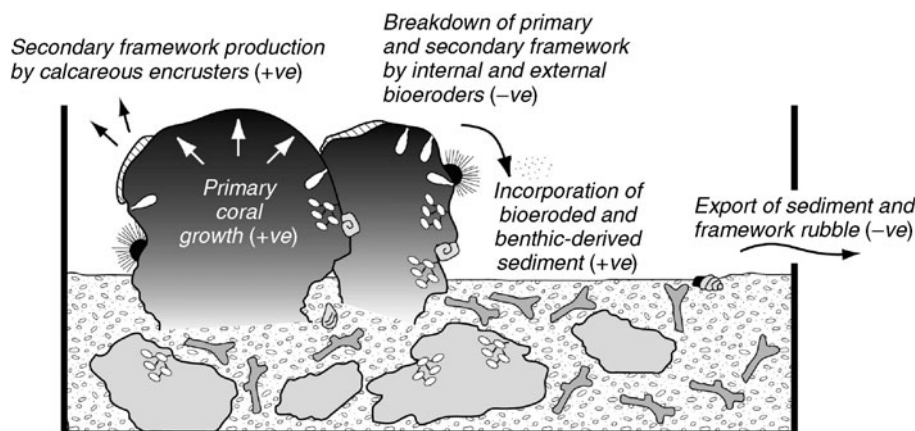
$P_{\text{sf}}$  = Secondary framework carbonate production.

$P_{\text{e}}$  = Primary and secondary framework carbonate lost to erosion.

$\text{Sed}_i$  = Sediment incorporated into the reef framework (includes both benthic carbonate sediment and by-products of framework erosion less that exported from the reef).

Several detailed studies have quantified net rates of carbonate production, using carbonate budgets approaches, at the reef system scale, and these including studies on Caribbean reefs in Barbados ( $4.48 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ; Scoffin et al., 1980) and St. Croix ( $0.91 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ; Hubbard et al., 1990), and in the Indo Pacific in Hawaii ( $0.89 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ; Harney and Fletcher, 2003) and Indonesia (ranging from  $11.68$  to  $-7.6 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$ ; Edinger et al., 2000). Several studies have also utilized census-based budget approaches to quantify rates of sediment production within reef-related sedimentary environments. These include estimates of reef island sediment production (Hart and Kench, 2007), and epiphytic carbonate production in seagrass beds (Nelson and Ginsburg, 1986; Perry and Beavington-Penney, 2005). It is relevant to note that rates of carbonate production on shallow-water reefs have also previously been estimated using measures of alkalinity change in the waters overlying reefs (see Chapter *Density and Porosity: Influence on Reef Accretion Rates*). This approach provides an estimation of total carbonate production and early dissolution (Smith and Kinsey, 1976), and while resultant production estimates are in broad accord with the gross production estimates determined in process or census-based studies, it is not possible to quantify the production and erosion rates associated with individual organisms and/or processes. The approach thus has





**Carbonate Budgets and Reef Framework Accumulation, Figure 1** Schematic illustrating the main production (+ve) and erosional (–ve) processes that determine a reef's carbonate budget.

significant merit but provides a different suite of data to census-based studies and does not enable the relative importance of different producer/eroder groups to be quantified.

#### Variations in carbonate production at the reef system scale

One important aspect of considering reef carbonate production from a carbonate budget perspective is the ability to quantify inter-reef variations in styles of reef framework accumulation. Kleypas et al., (2001), for example, highlighted a range of conceptual reef states that directly relate to variations in relative rates of carbonate production, sediment import and export and framework erosion. These different states demonstrate how shifts in the relative importance of individual processes, associated with different types of reef-building environments or environmental conditions, can result in fundamentally different reef budgetary states and reef framework structures. Production-dominated reefs, for example, exhibit rates of *in situ* biological  $\text{CaCO}_3$  production far in excess of rates of carbonate degradation and thus the budget is positive. This state is consistent with the rapid vertical growth trajectories exhibited by “keep-up” or “catch-up” reefs during the Holocene sea-level rise. In contrast, import-dominated reefs contain a high proportion of sedimentary material that is often terrigenous in origin. These reefs also have positive budgets, and good examples include the reefs described from the inner-shelf areas of the Great Barrier Reef in Australia (Smithers and Larcombe, 2003), Thailand (Tudhope and Scoffin, 1994) and Mozambique (Perry, 2005). Bioerosion-dominated reefs exhibit negative budgets with primary and secondary carbonate production being exceeded by biological substrate degradation. Examples include areas of high carbonate turnover, such as the non-framebuilding coral communities described from Oman (Benzoni et al., 2003) and the Red Sea (Riegl and Piller, 2000). Similar erosion-dominated states may also arise where non-calcifying groups become dominant and rates of carbonate production are reduced. A good

example of this has been described from the reefs around Uva Island, offshore Panama (Eakin, 2001).

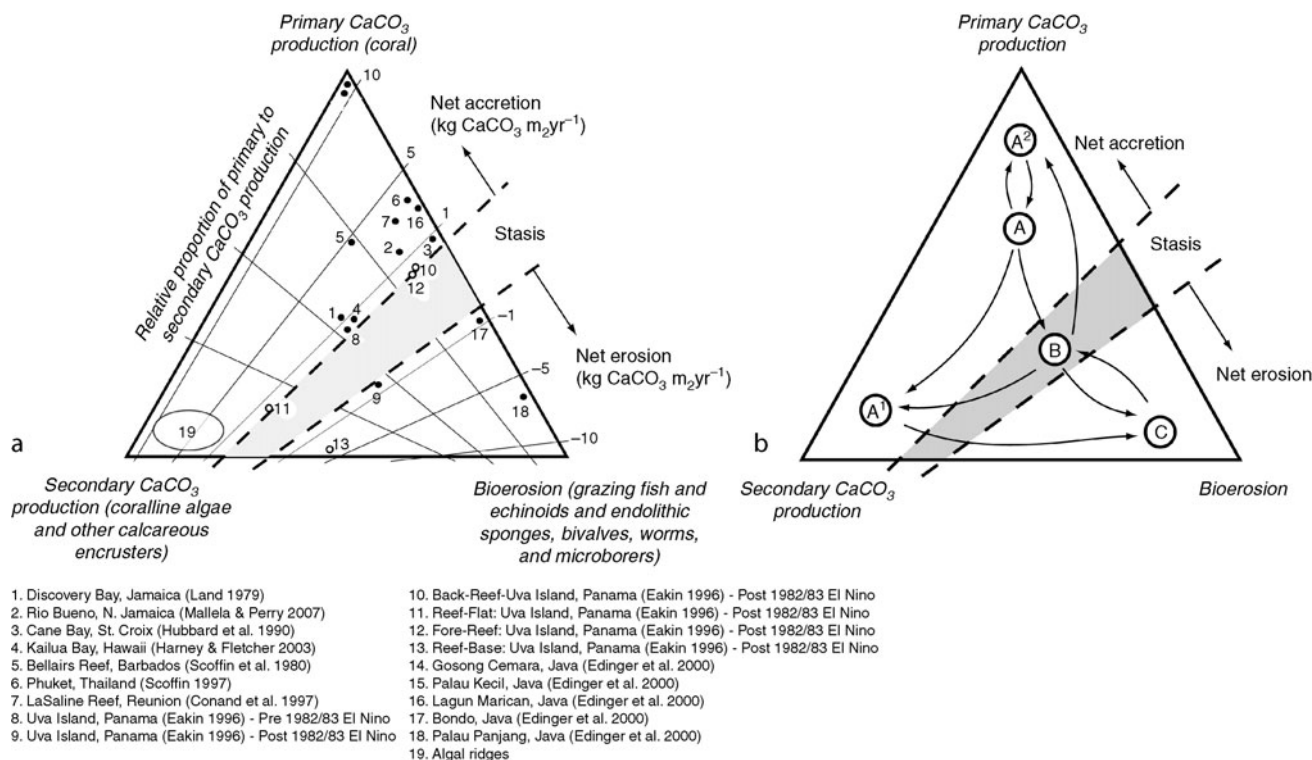
#### Carbonate budgets and long-term rates of reef framework accumulation

The conceptual budgetary states discussed above provide a framework for understanding the influence of carbonate production and erosion processes on reef accretion potential and framework fabric development at the system scale. In reality, however, framework types and their production rates are likely to vary markedly within different reef sub-environments (reef crest, shallow reef front, reef slope, etc.) depending upon the composition and abundance of coral species, species growth rates and, variations in the types and rates at which different productional and erosional processes operate. Perry (1999) illustrated spatial variations in the relative importance of these various processes and the resultant framework fabrics across a fringing reef system in north Jamaica, and these intra-reefal variations are also evident in budget assessments conducted in different areas of individual reef systems (Eakin, 1996). Over longer (millennial) timescales, these variations aggregate to determine net framework accumulation rates that are evident in many reef core records. Data available from many reefs on Australia's Great Barrier Reef demonstrate a relatively consistent relationship between facies type and net long-term accretion rates; highest rates ( $> 8 \text{ m ka}^{-1}$ ) occurring in branched coral facies, intermediate rates (typically  $< 5 \text{ m ka}^{-1}$ ) occurring in head coral facies, and the slowest rates ( $< 2 \text{ m ka}^{-1}$ ) occurring within algal crust facies (Hopley et al., 2007). These datasets also demonstrate marked changes in framework accretion rates during different phases of reef growth, with slow net accretion immediately following initiation, highest rates occurring as reefs accreted under rapidly rising sea levels, and slow or suppressed rates as reefs reach sea level. These variations reflect the carbonate production states and processes associated with different phases of reef development and

can thus be viewed as an interplay between community states (and thus net carbonate production rates) and sea-level position. It follows from this that different sea-level histories in different regions should be reflected in different accretion rate histories. For example, because Caribbean reefs have only recently reached present sea level (e.g., Toscano and Macintyre, 2003), the Late Holocene period has been characterised by vertical framework accretion and positive carbonate budgets. In contrast, sea levels in the Western Indo-Pacific region were attained ~6,000 years ago (with some reefs also then subjected to somewhat higher than present levels and subsequent sea-level fall e.g., Smithers et al., 2006). Thus in the Indo-Pacific, the Late Holocene period has been associated with dramatically reduced rates of carbonate production and vertical accretion (Hopley et al., 2007).

### Using carbonate budgets to monitor changes in reef "health"

As outlined above, the balance between processes producing  $\text{CaCO}_3$  and those removing it or converting it to sediment exerts an important influence on net rates of reef carbonate production and accumulation at a range of scales in time and space. Transitions in the rates at which any of the individual, or combined processes (either constructive or destructive) operate consequently have important implications for reef structures and reef-associated sedimentary landforms because they may shift the balance of the carbonate budget. Such changes may be driven either by direct anthropogenic activities (see Done, 1999; Hallock, 2001), or by climate-change induced shifts in sea level, temperature or seawater chemistry. All have the potential to modify the ecological functioning of reefs - changes that are



**Carbonate Budgets and Reef Framework Accumulation, Figure 2** (a) Ternary diagram showing different carbonate production states determined by variations in the relative importance of primary (coral) and secondary (calcareous encruster) carbonate production and carbonate breakdown to sediment/dissolution by bioerosion. Budget state points occupied by different reefs at the reef-wide scale (*closed circles*) and the reef sub-environment scale (*open circles*) where appropriate carbonate budget data exists are shown. (b) Conceptual model showing hypothetical transitions and potential pathways in reef carbonate production states driven by ecological or environmental change. Points A and A<sup>1</sup> are analogous to "production-dominated" reef states with production dominated by corals and calcareous encrusters, respectively. Point C is analogous to a "bioerosion-dominated" state. Subtle transitions in production status (e.g., A-A<sup>2</sup> and vice versa) may occur due to intermittent disturbance events where the relative importance of carbonate producers and/or the ratio of production to bioerosion changes, but the system is still one of positive net production. In some cases, reefs may shift from states of net accretion to net erosion (pathway A-B-C). Cessation of disturbance or an adaptation of the coral community (e.g., recruitment of, or replacement by, new, better adapted species) may allow transitions back to conditions of high carbonate production, with either similar (pathway C-B-A) or modified net production rates (C-B-A<sup>2</sup>). Adapted from Perry et al. (2008).

consistent with the “phase shift” concept (Done, 1992) – and thus to alter the carbonate depositional system. Such changes clearly demonstrate the potential for reef budget states to shift from positive (accretionary) to negative (erosional), a concept illustrated in recent studies of both anthropogenically impacted reefs in Indonesia (Edinger et al., 2000) and those impacted by El Nino-related sea-surface temperature fluctuations in the Eastern Pacific (Eakin 1996; 2001). In both cases, elevated rates of bioerosion have lead to shifts from positive to negative budgetary states, and emphasize the potential value, to reef health assessments, of quantifying budgetary components on coral reefs.

These concepts were recently developed by Perry et al. (2008) who proposed a framework production states approach that integrates assessments of the three key carbonate budget process groupings; primary production by coral, secondary production by calcareous encrusters, and bioerosion. The approach allows different states of reef production to be plotted within a ternary space (each process defining one corner of the ternary space; Figure 2a) and delineates areas of net accretion, net erosion, or accretionary stasis. One of the potential advantages of this approach is that it allows the relative importance of different process groups to be considered, thus acknowledging that while corals often dominate carbonate production, in some reef settings it is the calcareous encrusters (especially the coral-line algae) that make an equal or greater contribution to reef framework production. Similarly, appropriate consideration can be given to the role played by bioeroders in determining net carbonate production rates. This ternary approach also provides a useful mechanism for tracking temporal variations in the budgetary states of individual reefs, especially where ecological shifts (driven by either intrinsic or extrinsic factors) may modify the relative production rates or the abundances of carbonate producers/eroders (Figure 2b). This approach compliments the coral-macroalgal shifts identified within ecological reef phase shift models by encompassing transitions in carbonate production states resulting from different community states and disturbance regimes.

## Summary

A carbonate budget is a quantitative measure of the net rate of carbonate production on a reef (or within a carbonate sedimentary environment). The approach relies on census-based measures of the different producer and eroder groups on a reef – the individual measures of production and erosion being summed to determine net production rates per unit area of reef surface (typically expressed as a measure in  $\text{kg CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$ ). The use of carbonate budgets, although methodological complex, has considerable conceptual merit for understanding spatial and temporal variations in styles of reef framework development. Budgets also have considerable quantitative merit for determining production states at a given point in time and for tracking temporal shifts in carbonate productivity (e.g., production to erosion-dominated states) such

as may result from both intrinsically and extrinsically-driven environmental change.

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## Cross-references

Bioerosion  
 Corals: Biology, Skeletal Deposition, and Reef-Building  
 Density and Porosity: Influence on Reef Accretion Rates  
 Floatstone  
 Framestone  
 Packstone  
 Rudstone  
 Sea Level Change and Its Effect on Reef Growth  
 Submarine Lithification  
 Taphonomy

## CARBONIFEROUS REEFS

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### Definition

All reefs, which formed during the Carboniferous period (ca. 359–299 Ma). The Carboniferous is the longest period of the Phanerozoic Eon. It was named after the abundance of Coal-bearing strata in its upper half.

Although the geological perspective has to be considered, the Carboniferous period shows considerable overlap to modern times. Reefs formed during times of profound global changes – greenhouse to icehouse climates, dramatically changed continent configuration during the process of supercontinent formation, and important and frequent sea level changes to name only a few of them. Timing and duration of reef development and their dimensions varied considerably on a regional scale, but on the global scale reefs developed throughout the entire Carboniferous period (Aretz and Vachard, 2007). Overall reef abundance was more common than what has been often postulated, but lower compared to peak times of reef development in the Middle Palaeozoic (Webb, 2002).

Characteristic is the lack of a stable reef community. A broad range of bioconstructors – microbial communities, calcareous and siliceous sponges, rugose and tabulate corals, bryozoans, brachiopods, and calcareous algae – contributed in varying abundances to different stage of reef development (as initiation, formation, stabilization, and domination). However, microbial communities were very abundant and crucial for many Carboniferous reefs.

Reefs occurred along a bathymetric gradient from the intertidal/subtidal interface to several hundred meters of depth. Very different reef types developed from small undifferentiated patch-reefs to atoll reefs on oceanic sea mounts to reef tracts along shelf margins. The scarcity of the latter had an important influence on the geometry of many Carboniferous shelf systems.

Individual reef development reflects the local and/or regional tectono-sedimentary environments, but climate seems to be the most important global driving force. Major re-organisations in the reef environments occurred at the base of the Carboniferous, around the Mid-Carboniferous boundary, and at the base of the latest Carboniferous.

The oldest reefs are shallow water microbial reefs near the base of the Carboniferous in Eastern Australia. Mud-dominated mounds and buildups often labeled as Waulsortian Mounds developed in deeper ramp settings of many tropical and subtropical shelf systems of Early Carboniferous age. Often they rose into the photic zone, which resulted in a marked biodiversity increase in the vertical profile of the individual mound. Contemporaneous reefs in shallow waters formed by the above mentioned

organisms in various abundances were wide spread in Gondwana, Laurussia, Armorica, Kazakhstan, China, and in the Panthalassa Ocean.

After climate cooling in the Mid-Carboniferous, corals did not contribute to reef formation any more. In the tropics and subtropics various calcareous algae (tubular algae, phylloid green algae and red algae) and chaetetid sponges contributed to the formation of three basic types. In somewhat more temperate waters pelmatozoans, bryozoans, brachiopods, and microbial communities were the main contributors to the formation of reefal/reef like structures (Wahlman, 2002).

In the latest Carboniferous period, following a short global warming, reefs of the tropical Tethyan realm consisted of calcareous algae and calcareous sponges, whereas in subtropical to temperate waters *Palaeoaplysina* mounds occurred in shallow settings and bryozoan-*Tubiphytes* reefs in deeper settings (Wahlman, 2002).

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## Cross-references

[Algae-Macro](#)  
[Atolls](#)  
[Barrier Reef \(Ribbon Reef\)](#)  
[Binding Organisms](#)  
[Climate Change and Coral Reefs](#)  
[Corals: Biology, Skeletal Deposition, and Reef-Building](#)  
[Devonian Reef Complexes of the Canning Basin](#)  
[Sea Level Change and Its Effect on Reef Growth](#)  
[Sponges](#)

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## CAY FORMATION

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### Definition

A cay (sometimes spelled key or quay) is a small, low elevation island composed of coral reef detritus of rubble or shingle and/or sand sized materials that have accumulated on the reef top surface.

### Formation

Cays are formed when ocean waves and tidal currents transport loose sediment across the reef top surface to a depositional node where concentration occurs and the sedimentary pile rises above the high tide (Hopley, 1981; Gourlay, 1988). Over time soil and vegetation may develop on the cay surface. This process is assisted by the presence of extensive sea bird populations and their associated guano deposition, which acts as a fertilizer for the developing vegetation.

There is a basic division of cays into windward shingle cays and leeward sand cays or mixed shingle/sand cays depending on the surface area and size of the associated reef top.

Stoddart and Steers (1977) seminal study of cays and the subsequent study by Stoddart et al. (1978), showed that cays on reefs of the Great Barrier Reef vary from small ephemeral sand patches emerging only at low tide to variable sizes of vegetated sand and shingle or mixed sand/shingle cays to the complex low wooded islands which are characterized by variable development of mangrove vegetation (McLean and Stoddart, 1978; Stoddart, 1965, 1969). The classification scheme of Stoddart and Steers (1977) is applicable throughout the various reef provinces (Indian Ocean, Maldives, Indonesia, Central Pacific Ocean, Fiji, Samoa, Polynesia, atolls; Atlantic Ocean, Caribbean, etc). One variant of the mixed sand/shingle cay type are called motus. This variety, unlike the sand-shingle cays that are molded by wave refraction, lie on unbroken reefs on atoll rims. They are formed by the deposition of shingle on the windward edge as storm boulder ridges. Such ridges serve as an anchor to further leeward deposition of sand-sized sediment (Nunn, 1994). Dickinson (2001; 2009) suggests that many of the Pacific Ocean motus are in fact “pinned” to the elevated abandoned reef flat which developed during higher-than-present sea levels during the mid-Holocene period.

Hopley et al. (2007, p.364, Fig. 10.16) have provided a summary of the attributes and frequency of reef types and cays on the Great Barrier Reef Province.

The cays are subjected to a range of physical, biological, and chemical variables that influence the morphological development (Flood, 1977, 1980, 1981, 1986; Umbgrove, 1947; Hopley, 1982, 1997; Chivas et al., 1986). Once the cay extends above the limit of high tide the wind action commences and the dry sands of the upper beach are transported inland to form dunes. This wind action produces an asymmetrical cross profile of the cay with a higher elevation on the windward side. Dunes of up to three meters elevation are not uncommon. Once colonized by pioneer vegetation and the presence of nesting colonies of sea birds, the humic and fertility content of the soil increases and larger vegetation such as shrubs and trees commence to grow. In addition, once the cay reaches a critical size, a fresh and/or brackish lens may become established towards the center of the cay.

The groundwater flow is usually radial from the core of the cay outward toward the beach (Vacher and Quinn, 1997). In the intertidal beach zone, interstitial seawater evaporates and calcium carbonate in the form of aragonite is deposited in the interparticulate pores of the beach sediments to form beachrock (Stoddart and Cann, 1965). Also, where large colonies of sea birds are resident over long periods their guano can cement and/or replace the cay sediments to produce phosphate rock or cay rock.

Serial changes in cay vegetation have been reported (Flood and Heatwole, 1986) as well as changes in their shape related to climatic fluctuations (Flood, 1986) and the impact of tropical cyclones (Flood and Jell, 1977; Scoffin, 1993; Verstappen, 1954; Woodroffe, 1993). There is considerable anxiety being expressed by those Indian Ocean and Pacific Island nation people who live on the low lying coral cays. They are concerned about the predicted climate changes and sea level rise (Woodroffe et al., 1990). Any sea level change will impact on the sediment source and the supply of sediment to and from the cay (Kench et al., 2005). Predicting the present and future stability is a challenging task for geomorphologists and engineers (Dickinson, 2001; 2009). Examples have been reported where the residual beach rock outcrops indicate the earlier presence of cays which were destroyed during hurricane/cyclone events.

The dates of Holocene sea level maximum for selected oceanic islands have been summarized by Nunn (1994) and Dickinson (2001) who found that in the millennia since 5,000 BP, no single scenario prevails and the observed patterns of sea level behavior vary depending on just where on the Earth the observations are made. This variability is related to the different properties and behaviors of the lithosphere.

## Summary

A cay is a supratidal feature developed on the reef top. It represents a stage in the evolutionary accumulation of reef derived detritus commencing as a subtidal bank, developing further as an intertidal bank, and then a supratidal island (unvegetated) to vegetated island (several steps in the complexity of vegetation).

A cay is the product of the interaction of the geological processes of sediment production, erosion, and transportation and the hydrodynamic process related to tidal processes and wave action (and cyclonic/typhoon/hurricane activities). Usually on oval or elongate platform reefs, the nodal point where the current/wave action energy decreases and sediment accumulates is situated on the reef top and not beyond the reef top in the area of the leeward sediment wedge.

The action of oceanic birds is of paramount importance in transporting seeds to colonize the surface of the cay; the dead vegetation adds to the humic deposits thereby enhancing the possibility of vegetation further colonizing the surface of the cay. Guano material also enhances the fertility of the soil profile, and around the beaches of the

cays beach rock, may form in the subsurface. On the larger cays, a freshwater/brackish water lens can develop and enhance the vegetative growth from shrubs to extensive forests of *Casuarina* and *Pisonia* trees.

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## Cross-references

[Atoll Islands \(Motus\)](#)  
[Beach Rock](#)  
[Coral Cay Classification, and Evolution](#)  
[Coral Cays Geohydrology](#)  
[Coral Cays, Vegetational Succession](#)  
[Low Wooded Islands](#)  
[Unvegetated Cays](#)

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## CHAMISSO, ADELBERT VON (1781–1838)

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By the end of the eighteenth century, investigation into the major problems of reef formation and the nature of coral “insects” had advanced considerably: the definitive investigations by Peysonnell resulted in general agreement that reefs were created in some way by minuscule polyps. Aboard the cruise of the *Adventure* to Tahiti by Cook was the German naturalist Johann Reinhold Forster (1729–1798) who distinguished a fundamental feature of atolls, namely that the formation of a circular structure enables the coral colonies to resist the rage and power of the ocean.

In the same period, once they gained control of the North Pacific with their ice-free port of Vladivostock, the Russians also became active. Of early significance were the findings of Adelbert von Chamisso, born in France and later settled in Berlin, the naturalist who sailed on the first voyage of the Russian ship *Rurik* in 1815–1818 under the command of Otto von Kotzebue

around the Pacific to the Hawaiian, Marshall and Mariana groups. In an account entitled “On the Coral Islands” in an appendix to Kotzebue’s narrative of the voyage, Chamisso made two important observations.

Firstly, he pointed out that corals thrive best in windward, turbulent reef fronts, stating that the larger species of corals, which form blocks measuring several fathoms in thickness, seem to prefer the more violent surf on the external edge of the reef a point amplified further on, that the windward side of the reef, exposed to the unremitting fury of the ocean, should first rise above the element that created it. His second observation attempted to explain why atolls appear in wide expanses of turbulent oceans, almost out of nowhere: because, he reasoned out, that the corals have founded their buildings on shoals in the sea; or to speak more correctly, on the tops of mountains lying under the water, and that, even further, variation in magnitude and distribution of atoll clusters probably depends on the size of the sub-marine mountain tops, on which their basis is founded.

Once back in Russia, Kotzebue published his findings in German in 1821 in three volumes under the general title *Reise um die Welt* (Voyage around the World), Chamisso writing much of the third volume, which became available to English geologists in a translation the same year.

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## Cross-references

[Cook, James \(1728–1779\)](#)  
[Peysonnell, Jean-Andre \(1694–1759\)](#)

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## CLASSIFICATION OF CARBONATES

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## Definition and introduction

Rocks are classified in order to communicate information about them. Limestone classifications are often intended to convey information about the composition and so, the depositional setting. All classifications of limestones tend to be rather arbitrary and they frequently overlap or do not fit one’s particular needs. Since binocular microscopes or hand lenses are the tools that are commonly available to the professional or academic geologist, a practical

classification should be based on descriptions that use these tools. When these instruments are used, it is usually possible to identify the individual grains forming the rock. Thus, most classifications require that the most significant sedimentary particle in the rock be described. For instance, if a rock is composed of ooids, it is termed an oolitic limestone. If the limestone also contains a minor element such as skeletal fragments, then it is called a skeletal-oolitic limestone.

Two of the most widely used classifications are those of Folk (1959, 1962) and Dunham (1962). Both classifications subdivide limestones primarily on the basis of their matrix content and their major component grains.

Most limestones are classified by Folk (1959, 1962) as allochemical rocks if they contain over 10% allochems (transported carbonate grains). Based on the percentage of interstitial material, the rocks may be further subdivided into two groups: sparry allochemical limestones (containing a sparry calcite cement of clear coarsely crystalline mosaic calcite crystals) and microcrystalline allochemical limestone (containing microcrystalline calcite mud, micrite, which is subtranslucent grayish or brownish particles less than about 5  $\mu\text{m}$  in size) (Figure 1). Further subdivision is based on the allochem ratios of Folk (1962) as is illustrated in Scholle and Ulmer-Scholle (2003) (Figure 2).

Thus, Folk's classification (Figures 1 and 2) is most suited for thin section study. Note that he terms rocks with appreciable matrix as micrites while matrix-free rocks that contain sparry calcite cement are termed sparites. Sparites and micrites are further subdivided on the basis of their most common grains.

In contrast, Dunham's classification (Figures 3 and 4) and its modification by Embry and Klovan (1971) and James (1984) update and illustrations deal with depositional texture. For this reason, Dunham's scheme is better suited for rock descriptions that employ a hand lens or binocular microscope. For example, if the grains of a limestone are touching one another and the sediment contains no mud, then the sediment is called a grainstone. If the carbonate is grain supported but contains a small percentage of mud, then it is known as a packstone. If the sediment is mud supported but contains more than 10% grains, then it is known as a wackestone, and if it contains less than 10% grains and is mud supported, it is known as a mudstone.

If one compares the two classifications, a rock rich in carbonate mud is termed a micrite by Folk and a mudstone or wackestone by Dunham. Moreover, a rock containing little matrix is termed a sparite by Folk and a grainstone or packstone by Dunham. The wide range of percentage of mud matrix that a carbonate may have and still be termed a packstone by Dunham sometimes reduces the utility of this classification. Embry has modified the classification of Dunham and Klovan (1971) to include coarse grained carbonates (above figure). In their revised scheme, a wackestone in which the grains are greater than 2 mm in size is termed a floatstone and a coarse grainstone is called a rudstone.

Both terms are extremely useful in the description of limestones. Embry and Klovan modified the boundstone classification of Dunham in order to graphically express the role that organisms performed during accumulation. They introduced terms such as bafflestone, bindstone, and framestone, which are useful in concept, but these can be extremely difficult to apply to ancient limestones where diagenesis and sample size can limit one's ability to determine an organism's function.

Other modifications followed Folk's (1965) recognition that though micrite is more commonly a product of sedimentary accumulation, it can also be cement, and/or a product of diagenesis. To this end, Reid et al. (1990) and Wright (1992) and others are not alone in reemphasizing the need to recognize the role of micrite and other allochems as a product of sedimentary matrix, internal cavity sedimentary fill, diagenesis, and cementation, and that some carbonate grains are the products of later diagenetic modifications. The reader is urged to recognize the multiplicity of origins of carbonates, though their sedimentary origin is commoner.

### A short history of limestone classifications

The classification of limestones has been constantly updated as new analytical techniques have been developed and new information has become available. This has resulted in new understandings about the origin and depositional setting of carbonate particles and carbonate sediments.

Limestone classifications underwent a rapid evolution shortly after Wolf (1961) published an excellent summary of the early classification schemes for carbonates. In this, he recognized that many of these classifications unfortunately were inefficient and commonly misleading; in particular, the descriptive terms used to describe carbonates included detrital, clastic, fragmental, granular, fossiliferous, calcarenite, coquina, etc. Each one of these terms conveys one particular aspect of information, but ignored, among other things, the presence or absence of cement or matrix.

Earlier classifications include Twenhoffel's of 1932 which recognized three major limestone groups:

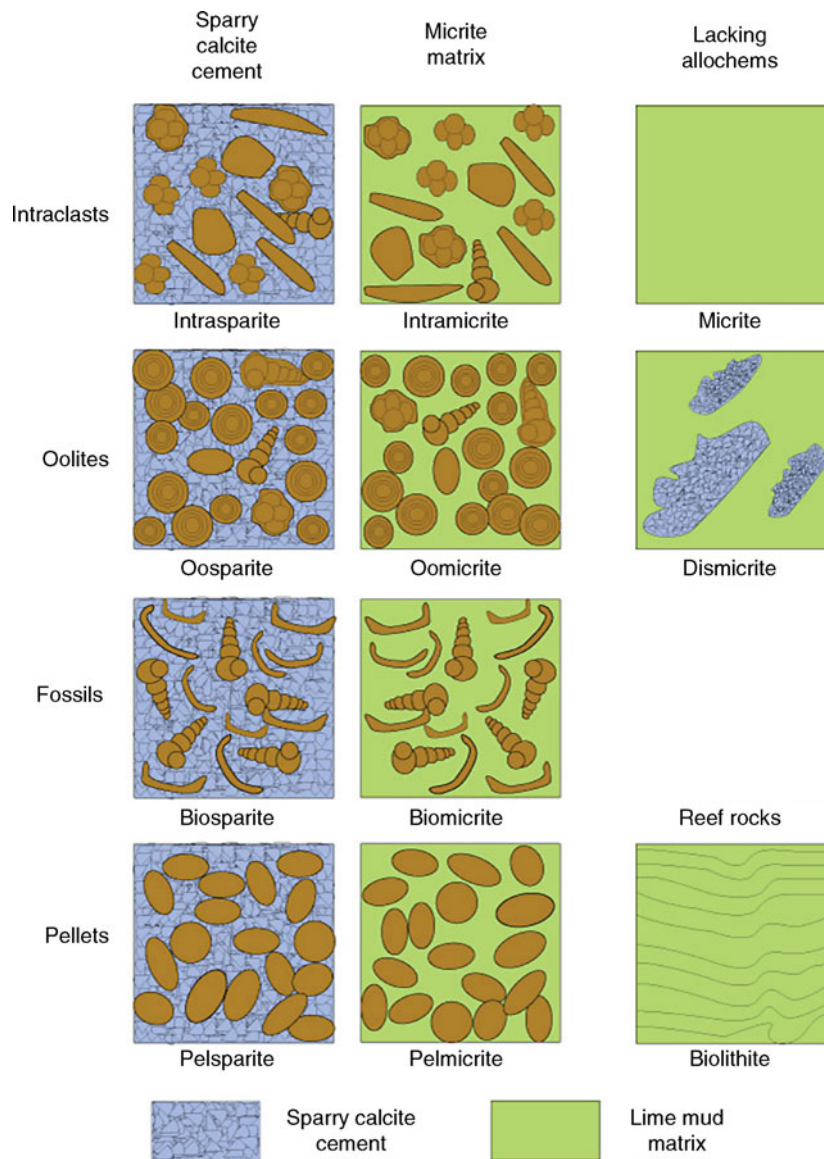
1. Organic origin
2. Chemical origin
3. Mechanical origin

In the 1930s, workers differentiated between the following types of limestones:

1. Hard
2. Mud or soft

In the 1950s, workers recognized:

1. Uncemented
  - (a) Calcilutites (mud sized)
  - (b) Calcarenites (sand sized)
  - (c) Calcirudite (gravel sized)
  - (d) Mixture of (a), (b), and (c).
2. Primary hard (chemical or biochemically cemented)
3. Secondary hard (diagenetically modified)



C.G.St.C. Kendall, 2005 (after Folk 1959)

**Classification of Carbonates, Figure 1** Folk (1962) limestone classification table identifies the component (or allochemical) particles and whether the matrix is micrite or lime mud or a sparry calcite cement precipitated between the grains. Should intraclasts form >25% of the grains, then the rock is named an intraclastic limestone; if intraclasts are <25% and ooids are >25%, the rock is an oolitic limestone; if intraclasts and ooids are <25% each, then the rock is known as a biogenic, or skeletal, or pelletal limestone, according to the relative percentages of these allochemical grains. Limestones with multicomponents are named after these mixtures (e.g., a biopelsparite). A dismicrite is a micrite with spar-filled blebs (generally burrows) and a biolithite is a biologically bound rock.

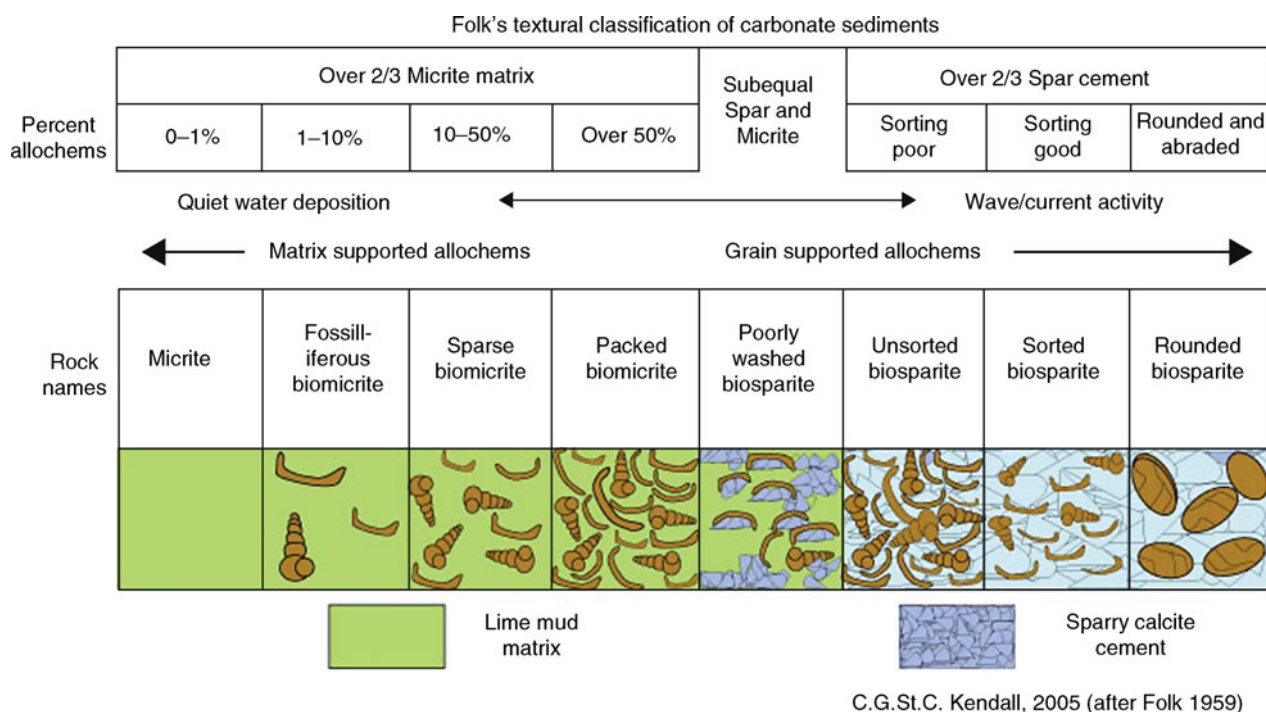
In the late 1950s and early 1960s descriptions were based on size nomenclature, namely, calcilutite, calcarenite, and calcirudite. Others used calculite and calcisiltite for mud and silt sized, respectively. The work of Illing (1954), Folk (1959), Carozzi (1960), Dunham (1962), Embry and Klovan (1972), and James (1984) addressed these shortcomings and the two commonly accepted schemes that evolved from these are used today in industry

and academia. As explained above, these are based on the classification schemes of Folk (1962) and Dunham (1962).

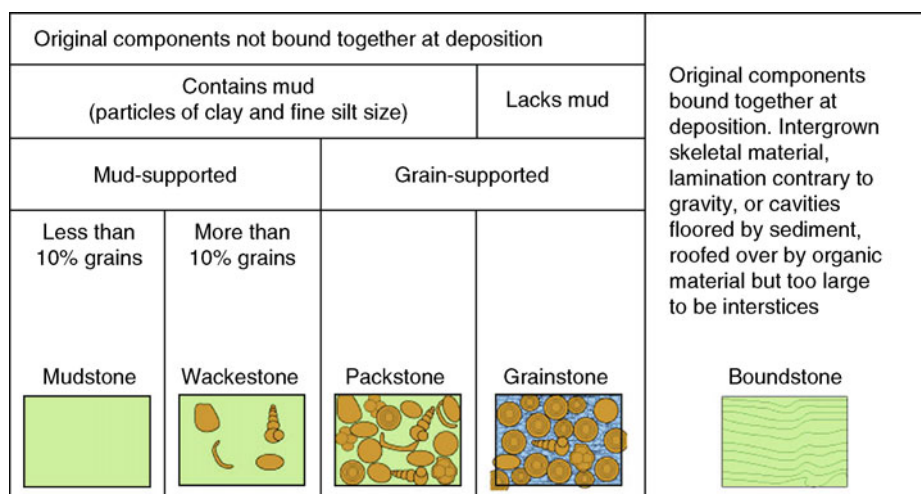
Pettijohn (1952) divided limestones into two groups:

1. Autochthonous – formed in situ by biochemical processes
2. Allochthonous – consisting of transported and redeposited material.





**Classification of Carbonates, Figure 2** Folk's (1962) textural spectrum for carbonate sediments records 8 phases of sorting and rounding with the intent of capturing the deposition settings from low energy (*left*) to high energy (*right*). In very low-energy settings, micrites or mud-sized carbonate accumulate; in intermediate-energy settings, micrites with greater concentrations of allochemical particles, winnowed grain, and mud accumulations result; in high-energy settings, sorting and rounding of grains winnow most of the micrite matrix away. Textural inversions are the result of storm events that mix sediments from different settings or introduce short-lived conditions into a normally low-energy setting.



C. G. St. C. Kendall, 2005 (after Dunham, 1962, AAPG Memoir 1)

**Classification of Carbonates, Figure 3** Dunham's 1962 classification of carbonate rocks is intended to convey information related to their depositional setting. Carbonates that are supported by matrix (mud) or framework (grains) form the basis of this classification. The end members include noncrystalline limestones often characterized by referencing the major component grains.

| Allochthonous                                           |                             | Autochthonous                                       |                                    |                                            |
|---------------------------------------------------------|-----------------------------|-----------------------------------------------------|------------------------------------|--------------------------------------------|
| Original components not bound organically at deposition |                             | Original components bound organically at deposition |                                    |                                            |
| >10% grains >2mm                                        |                             |                                                     |                                    |                                            |
| Matrix supported                                        | Supported by >2mm component |                                                     |                                    |                                            |
|                                                         |                             | By organisms that act as baffles                    | By organisms that encrust and bind | By organisms that build a rigid frame work |
| Floatstone                                              | Rudstone                    | Bafflestone                                         | Bindstone                          | Framestone                                 |

Textural classification of reef limestones after Embry & Klovan (1971) and James (1984)

**Classification of Carbonates, Figure 4** Embry and Klovan (1971) modification of the Dunham's (1962) biologic classification of organically bound rocks. "Floatstone" replaces Dunham's "packstone"; the term "rudstone" replaces grain-supported biogenic limestones, and other organically bound rock are termed "bafflestone," "bindstone," or "framestone," depending on the character of the organic structures. These latter terms are often used to describe the fabric of reefs, bioherms, and other biogenic carbonates.

The Allochthonous grains are usually sourced intraformational or certainly intrabasinal.

The early researchers appreciated the complicated nature of carbonate rocks. They classified them both on the basis of origin of the components and depositional textures. Carozzi (1960) also offered a classification scheme which recognized several subtypes of Autochthonous and Allochthonous varieties of carbonates.

It was Folk (1959) who first successfully presented a comprehensive carbonate classification. He divided limestones into autochthonous, the so-called biolithites, and allochemical, those composed of various types of grains and matrix or cement. One or more grains can be associated with lime mud (= micrite) or lack micrite and instead are cemented by sparry calcite (= sparite). This classification has genetic implications and hence the conditions of the depositional setting and the formation of the grains are inferred. Interpretations about the depositional setting are of fundamental significance to oil/gas exploration and hence this classification scheme has gained wide acceptance.

Dunham (1962) proposed another classification scheme that is used as much as Folk (1959, 1962) by the oil/gas industry. Both classifications distinguish allochems, matrix or micrite, and sparry calcite cement and both schemes emphasize texture (depositional texture and hence depositional setting). Both are widely used today with some modifications (Embry and Klovan, 1971; James, 1984) to the virtual exclusion of all other limestone classification schemes. Many geologists use the two schemes interchangeably. Concurrently, micrite is recognized both as a sedimentary matrix, internal cavity sedimentary fill, and as a diagenetic product and cement, while some carbonate grains are the products of later diagenetic modifications (Reid et al., 1990; Wright, 1992).

#### Application of the recommended carbonate classification schemes

Irrespective of the classification scheme used (Folk or Dunham), the first question one should ask when classifying limestone is "can the deposition texture still be recognized?"

We recommend that a step-by-step approach be used in the Dunham scheme. The order of questions to be asked is:

1. Is the depositional texture recognizable?  
No – called crystalline limestone  
Yes – go to 2.
2. Was the rock bound together during deposition?  
Yes – boundstone  
No – go to 3.
3. Components deposited as distinct grains  
Grain supported – no mud – grainstone  
Grain supported – some mud – packstone  
Mud supported > 10% grains – wackestone  
Mud < 10% grains – mudstone

This classification key can be represented in a diagrammatic way (see Dunham Classification Scheme diagram).

### Summary

A variety of classification schemes have been proposed for limestones that provide information relating to their origin, component composition, grain size, presence of matrix or cement, and depositional setting. The first universally accepted scheme was that of Folk, developed in 1959 to integrate the origin, component composition, grain size, and depositional setting. This was elaborated further in 1962. Folk's scheme is most suited for the study of thin sections of limestones.

An alternative classification scheme was proposed by Dunham in 1962. This is more suited for limestone descriptions made when using a hand lens or binocular microscope. It was further modified in 1971 by Embry and Klovan. Dunham's scheme is now commonly used by the oil/gas exploration industry.

A subsequent modification was proposed by James in 1984. It enables these various earlier schemes to be used interchangeably. The classification schemes can be represented in diagrammatic form.

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### Cross-references

[Bindstone](#)  
[Floatstone](#)  
[Framestone](#)  
[Micrite](#)  
[Packstone](#)  
[Rudstone](#)  
[Wackestone](#)

## CLIMATE CHANGE AND CORAL REEFS

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### Definition

Climate: Weather expected at given location and time of year, based on observations over at least 30 years, including average values and range of variability.

Climate change: Significant and persistent change in average and/or variability of climate.

Greenhouse gas: Constituent of atmosphere that absorbs and emits thermal infrared radiation.

Greenhouse effect: Trapping by atmospheric greenhouse gases of thermal infrared radiation, which otherwise would be lost to space, within climate system. Without the natural greenhouse effect, the earth would be about 30°C cooler and uninhabitable.

### A rapidly changing climate

Climate change is not new. Global and regional climate has varied and changed in the past on a range of time scales due to a variety of internal and external causes (IPCC, 2007a, Chap. 1). Organisms and ecosystems, such as coral reefs, have survived, changed their distribution, and adapted to many of these past changes.

We are, however, in a new era of rapidly changing global climate as a consequence of human activities. The evidence for increasing greenhouse gases due to burning of fossil fuels, land-use changes and agriculture activities since the late eighteenth century is unequivocal (IPCC, 2007a, Chap. 2). The atmospheric concentration of the main greenhouse gas, carbon dioxide (CO<sub>2</sub>), has risen about 40% from 280 ppm in 1750 to 383 ppm in 2007, the highest concentration of the last 650,000 years and possibly the last 20 million years. Not only



are atmospheric concentrations of greenhouse gases rising but also the rate of increase is accelerating (Canadell et al., 2007).

This increase in atmospheric greenhouse gases results in significant positive radiative forcing of the global climate system and global warming attributable to human activities. The most recent Intergovernmental Panel on Climate Change Fourth Assessment (IPCC-AR4) report provides observational and paleoclimatic evidence for significant recent warming of global climate that matches theoretical and modeled consequences of increased greenhouse gas concentrations (IPCC, 2007c). The relatively modest global warming observed to date has already been associated with changes in the global climate system such as more intense rainfall, more frequent droughts, sea-level rise, loss of Arctic sea ice, melting of land-based ice, and a widening of the tropical climate belt (IPCC, 2007a, Chap. 3; Seidel et al., 2007). The rate of warming is about twice as fast for land masses compared to oceans and for high latitudes of the Northern Hemisphere compared with that for low latitude regions. Observed changes in climate are driving changes in the world's biological and physical systems that are all consistent with a rapidly warming climate (IPCC, 2007b; Rosenzweig et al., 2008).

The observational record shows that the average global land and sea temperature climate of the most recent 30 years (1979–2008) is significantly warmer ( $+0.55^{\circ}\text{C}$ ) than the climate at the end of the nineteenth century (1871–1900; Figure 1a). The tropical oceans, home to the world's coral reefs, have also significantly warmed (at about 70% of the global average value) by  $+0.40^{\circ}\text{C}$  between the same periods (Figure 1b). The rate of warming has accelerated from  $0.05^{\circ}\text{C}$  (global) and  $0.04^{\circ}\text{C}$  per decade (tropical oceans), for the period 1871 to 2008, to  $0.12^{\circ}\text{C}$  (global) and  $0.08^{\circ}\text{C}$  per decade (tropical oceans) for the recent period 1950–2008.

Coral reef ecosystems, which occur in the naturally warm tropical oceans and are one of the largest sources of global marine diversity (Sala and Knowlton, 2006), are considered among the “most vulnerable ecosystems” to global climate change (IPCC, 2007b, Chap. 4, p. 214). This global-scale threat is occurring against a backdrop in which many of the world's coral reef ecosystems have already been degraded by direct human pressures. These local and regional stressors include overfishing, destructive fishing, and decline in water quality due to increased sediment, nutrient, and chemical pollution from changes in coastal land use (Hughes et al., 2003; Buddemeier et al., 2004). Fifteen years ago, a group of coral reef experts concluded that such “human pressures pose a far greater immediate threat to coral reefs than climate change, which may only threaten reefs in the distant future.” (Wilkinson and Buddemeier, 1994, p. VIII).

### Climate factors affecting coral reefs

#### Physical climatic environment of coral reefs: defining the envelope

To assess the consequences of change requires the understanding of present-day environmental controls on tropical

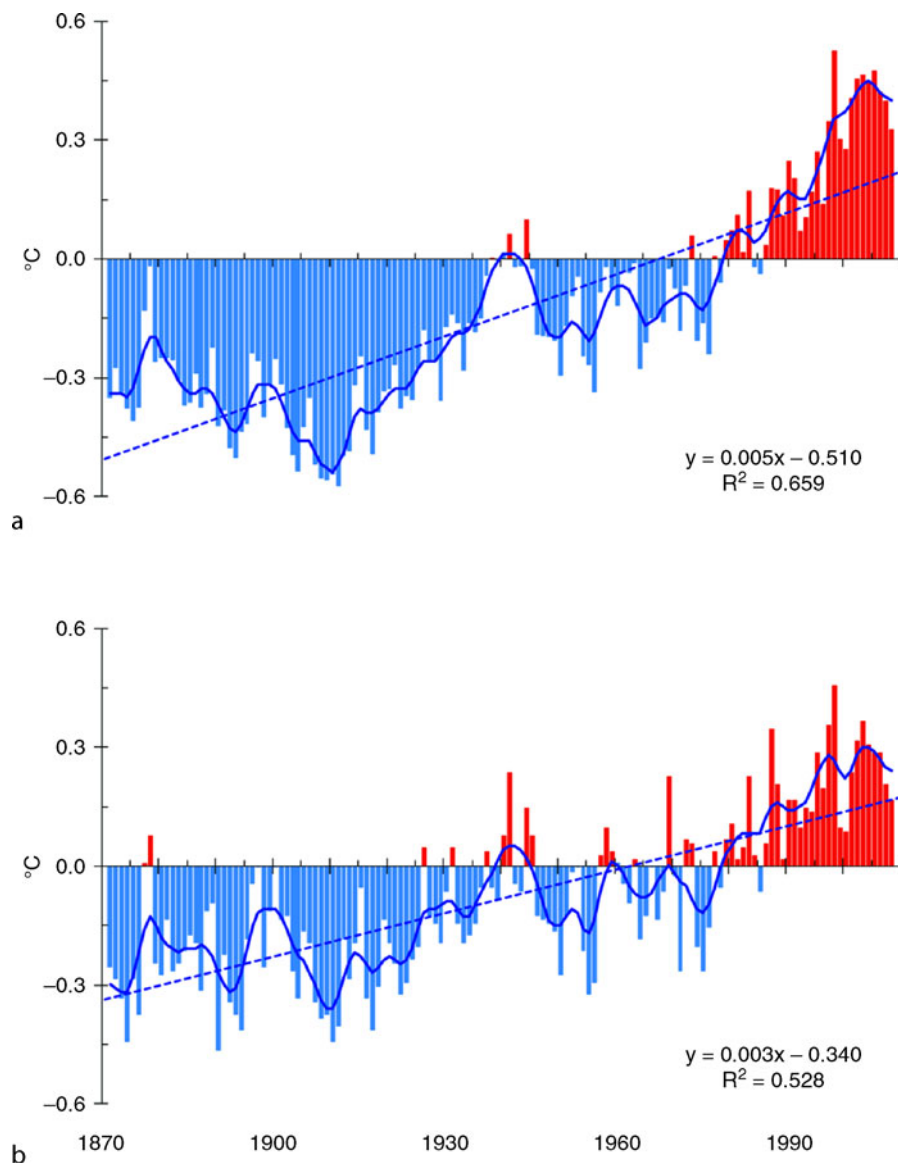
coral reefs (see also *Corals: Environmental Controls on Growth*). They are largely confined to shallow, warm, clear, and well-lit waters with  $18^{\circ}\text{C}$  identified as the minimum annual sea surface temperature (SST) necessary for reef growth and although upper thermal limits are less clear, nowhere, at present, is considered too warm for coral reef development (Achituv and Dubinsky, 1990). Comparing present-day distribution of nearly 1,000 reefs and a range of environmental variables, Kleypas et al. (1999a) found that the most important factors were warm SSTs (averaging  $27.6^{\circ}\text{C}$ ), high aragonite saturation (ranging from 3.28 to 4.06 and 3.83 marking the transition from coral reefs to non-reef-forming coral communities), and high available light. In general, present-day coral reefs live within a relatively narrow range of these three variables (Hoegh-Guldberg, 2005).

#### Other weather and climatic factors affecting coral reefs

Water temperatures, ocean chemistry, and available light thus broadly define, given suitable bathymetry, where coral reefs occur. Salinity and nutrient supplies are more regionally specific controls which are modulated by the amount of rainfall and freshwater flow into nearshore reef environments. Also regionally important are ocean circulation patterns that control larval supplies between reefs (connectivity) and upwelling of nutrients. Coral reefs span a range of environments from clear oceanic waters to low salinity and turbid waters near land (Fabricius, 2005).

Tropical cyclones (see *Tropical Cyclone/Hurricane*), the most destructive of the world's weather systems, are natural sources of disturbance to many coral reefs poleward of  $\sim 10^{\circ}$  from the equator (Emanuel, 2003). Tropical cyclones, through the large waves they generate, can directly affect and even decimate reef structures and coral assemblages as well as reducing salinity through heavy rainfall and causing coastal destruction associated with storm surges (Dollar, 1982; Massel and Done, 1993). Given time ( $\sim 10$ – $20$  years), and no other sources of environmental stress, coral reefs can recover from such local physical disturbances (Done, 1999; Hughes and Connell, 1999; Coles and Brown, 2007). In addition to the immediate physical impacts of tropical cyclones, their local occurrence has been shown in the Caribbean to have longer term consequences by limiting subsequent coral recruitment, survival, and compounding coral cover declines due to other factors (Gardner et al., 2005; Crabbe et al., 2008).

El Niño-Southern Oscillation (ENSO) events are the principle source of interannual global climate variability. This highly coupled ocean-atmosphere phenomenon is centered in the tropical Pacific producing significant climate and societal impacts throughout the tropics and some extratropical regions (McPhaden et al., 2006). ENSO fluctuates between two phases, El Niño and La Niña, each associated with distinct and different atmospheric and oceanic climate anomalies. From the perspective of coral reefs, the most significant of these anomalies are widespread warming of much of the tropical oceans during



**Climate Change and Coral Reefs, Figure 1** Annual anomalies (from 1961 to 1990 mean), 1871–2008 of (a) global average land and sea surface temperatures and (b) tropical average sea surface temperatures. *Thick line* is 10-year Gaussian filter emphasizing decadal variability. Linear regression line also provided (Data sources: HadCRUTV3, and HadISST2 <http://www.cru.uea.ac.uk>; Jones et al., 1999; Brohan et al., 2006; Rayner et al., 2003).

the evolution (typically over 12–18 months) of an El Niño event, as happened in 1982–1983 and 1997–1998. Both phases are also associated with changes in tropical rainfall amount and intensity (in particular floods and consequent increases in freshwater flows to nearshore reefs) and in preferred locations of tropical cyclone activity.

### Impacts of climate change on coral reefs

#### Warmer waters and coral bleaching

At the heart of tropical coral reefs is a mutually beneficial relationship between the coral animal and single-celled

photosynthetic plants. In return for protection and essential nutrients, the algae play a role in light-enhanced calcification and provide sufficient cheap energy to the coral host to allow rapid calcification and thus form the massive and complex carbonate structures of coral reefs (Barnes and Chalker, 1990; Veron, 2000). Coral bleaching describes the loss by the coral animal of all or some of these algae and their photosynthetic pigments so that the white calcium carbonate skeleton becomes visible through the translucent coral tissue. Coral bleaching is a response of the coral to an environmental stress such as unusually cold or warm temperatures, low salinity, or pollution.

Coral bleaching is not a new phenomenon due to global warming.

Corals live within 1–2°C of their upper thermal threshold, beyond which bleaching occurs (Coles et al., 1976; Jokiel and Coles, 1977). Currently maximum summer SSTs (the time of year when corals are most at risk from thermal stress) on coral reefs averages 29.5°C and ranges between 28.2 and 34.4°C (Kleypas et al., 1999a). There is not an absolute temperature at which corals bleach, rather (which is evidence of adaptation over the long term) the threshold varies with ambient SSTs (Berkelmans, 2002).

Observations off the Pacific coast of Panama in 1983 presented one of the earliest “most alarming” reports of “large-scale” bleaching of corals which was tentatively linked to the 1982–1983 El Niño (Glynn, 1983). Subsequent studies clearly linked these unusual events to warmer-than-usual SSTs (Brown, 1987; Glynn, 1996; Jokiel and Brown, 2004). What is new and now clearly associated with warming of the tropical oceans are mass coral bleaching events where entire reefs are affected and which can be locally attributed to unusually warm maximum SSTs (Smith and Buddemeier, 1992; Brown, 1997).

The real wake-up call regarding the sensitivity of corals to warmer waters was during the major El Niño event of 1997–1998 (McPhaden 1999) which coincided with the warmest year in global instrumental records (Hansen et al., 2006). Bleaching was reported from nearly every coral reef region and 16% of the world’s reefs was estimated to have been damaged (Wilkinson, 1998, 2004). The scale and magnitude of this event, during which impacts could be tracked round the world’s coral reefs as each reached its unusually warm seasonal SST maximum, catalyzed efforts both to understand and monitor conditions conducive to coral bleaching.

In an influential paper (Hoegh-Guldberg, 1999), mass coral bleaching events were firmly linked to warming of tropical seas as a result of climate change and, using global climate model (GCM) projections for selected locations, the author suggested that thermal thresholds for coral bleaching could be regularly exceeded within a matter of decades. Various studies have demonstrated that the level of thermal stress on coral reefs is closely linked to coral bleaching (e.g., Berkelmans et al., 2004) and that the level of this stress has been increasing as the tropical oceans warm (Lough, 2000; Barton and Casey, 2005; Sheppard and Rioja-Nieto 2005).

Several of the recent mass coral bleaching events have been associated with El Niño events (Williams and Bunkley-Williams, 1990). These do not cause coral bleaching but they increase the likelihood in many coral reef regions of thermal conditions conducive to coral bleaching (Lough, 2000; Eakin et al., 2009). Some reef locations, e.g., along the South Pacific Convergence Zone in the western tropical Pacific, are more likely to be unusually warm during the La Niña phase of ENSO [bleaching was observed here, e.g., during the 1998–1999 La Niña (Wilkinson, 2004)].

## Consequences of coral bleaching

A recent comprehensive review paper (Baker et al., 2008) summarizes much that we have learned and much that we still need to understand about the mass coral bleaching events that have affected many of the world’s coral reefs since the 1980s. As a consequence of bleaching, corals may fully recover, partially recover, or die, and there are a range of short- and long-term impacts on coral reef ecosystems. Examples include declines in abundance of coral- and reef-associated species, reduced coral growth rates, increased susceptibility of corals to diseases, enhanced rates of bioerosion, and impaired reproduction and recruitment.

The intensity and occurrence of coral bleaching associated with widespread thermal stress shows considerable variability. Bleaching is frequently more intense at the surface than on the sides of individual colonies, which implicates high light levels as a contributing factor (Salm and Coles, 2001; Brown and Dunne, 2008). Local weather conditions of slack winds, low cloud amount, and little water motion all favor both warming and increased light penetration through the water column. Different coral taxa show different thermal susceptibility, with branching corals often showing greater sensitivity than massive species (Marshall and Baird, 2000; McClanahan et al., 2004, 2005). Large-scale field surveys clearly demonstrate spatial clusters of more or less bleaching (Berkelmans et al., 2004; McClanahan et al., 2007a, b). Experimental studies suggest that high water motion can reduce the incidence of bleaching (Nakamura and Van Woesik, 2001; West and Salm, 2003; Smith and Birkeland, 2007). This is supported by field observations of reduced bleaching in regions of strong water motion due to tides, upwelling, mixing and wave energy (Salm and Coles, 2001; Skirving and Guinotte, 2001; Reigl, 2003), though in some locations high water flow has been suggested to reduce the corals ability to deal with thermal stress (McClanahan et al., 2005). Rapid cooling of SSTs by tropical cyclones can also locally reduce the occurrence and intensity of coral bleaching (Manzello et al., 2007).

Recovery from a bleaching disturbance is also variable across all spatial scales and across different coral reef communities (Golbuu et al., 2007; Baker et al., 2008). Some reefs recovered relatively rapidly from the catastrophic 1997–1998 event (e.g., Indian Ocean reefs), whereas others (e.g., Caribbean/western Atlantic reefs) continue to decline, due to ongoing local stressors. Lack of other local stressors is an important factor in determining how well coral reefs recover from bleaching (Sheppard et al., 2008). However, even with recovery of hard coral cover, there is evidence of differential recovery of various components of the original coral reef ecosystem, which results in a different community structure after the event (Smith et al., 2008). Key effects include loss of structural complexity and habitat, local extinctions, loss of biodiversity and key functional groups (Graham et al., 2006), and both immediate and long-term consequences



for corals themselves (McClanahan et al., 2009) and associated reef organisms (Pratchett et al., 2009).

An important question is to what extent corals and their symbionts maybe able to increase their tolerance to thermal stress with continued rapid global warming. Some argue that the potential for such successful adaptation on the time scales of observed and projected warming is limited (Hoegh-Guldberg, 1999, 2005). There is, however, experimental and observational evidence that some corals in some circumstances can and have increased their thermal tolerance by switching to a more thermally tolerant type of algal symbiont (Berkelmans and van Oppen, 2006; Goulet, 2006; Maynard et al., 2008; Oliver and Palumbi, 2009).

### Warmer water temperatures and coral diseases

Increased numbers of reports of diseases affecting marine organisms, including corals, have been tentatively linked to warming waters and El Niño events (Harvell et al., 1999). Coral disease outbreaks on the Great Barrier Reef (GBR) have been linked to temperature stress (Jones et al., 2004; Bruno et al., 2007), and experimental and observational studies show that coral black band disease is enhanced in warmer waters and high light conditions (Boyett et al., 2007).

### Warmer water temperatures: other effects

Warmer water temperatures can also directly affect physiological processes and distributions of corals and associated organisms. The northward range of two branching coral species has recently expanded in the western tropical Atlantic (Precht and Aronson, 2004). Coral community structure may change as juvenile corals grow more slowly and appear to die faster in warmer waters (Edmunds, 2004, 2007). Warmer temperatures have also been shown experimentally to affect larval supply, settlement, and survival (Negri et al., 2007; Nozawa and Harrison, 2007). Observational evidence of recent slowing in coral growth rates have also been linked to the combined effects of warmer waters and ocean acidification (De'ath et al., 2009; Tanzil et al., 2009).

### Changing ocean chemistry

A more insidious consequence, and potentially catastrophic (Veron, 2008), of increasing greenhouse gases for marine calcifying organisms is ocean acidification. About 30% of the extra CO<sub>2</sub> human activities have injected into the atmosphere has been absorbed by the oceans (Feely et al., 2004; Sabine et al., 2004) – if this had not happened, the earth would have warmed more than it has. Absorption of CO<sub>2</sub> lowers the pH, decreases the availability of carbonate ions, and this lowers the saturation state of the major shell and skeleton forming carbonate minerals (Kleypas et al., 2006). Observational and modeling evidence demonstrates ongoing decline in the aragonite saturation state of Caribbean waters over the period 1996–2006 (Gledhill et al., 2008). Lowering ocean

pH essentially shifts the balance of the geochemical equations whereby marine organisms, such as corals, calcify. Various modeling and experimental studies also demonstrate the reduced ability of corals to form their skeletal structures in more acidic waters (Kleypas et al., 1999b; Langdon and Atkinson, 2005; Orr et al., 2005; Doney et al., 2009).

Weaker coral reef structures reduce their structural resilience to the natural forces of erosion and a slower growth rate sets back recovery after disturbances. A recent experimental study suggests that ocean acidification can itself, and in combination with higher water temperatures, induce coral bleaching (Anthony et al., 2008). Ocean acidification affects not only corals (Guinotte and Fabry, 2008; Kuffner et al., 2008). Crustose coralline algae are particularly sensitive, and any setback to them may significantly undermine their vital role of cementing reef components together (Littler and Littler 1984; see also Chapter *Algae, Coralline*). The poorly cemented reefs of the eastern tropical Pacific (where aragonite saturation of waters is naturally low) may provide a picture of future coral reefs as the oceans continue to acidify (Manzello et al., 2008).

### Sea level

Global average sea level has risen by about 20 cm over the past century, primarily due to thermal expansion of the oceans and, to a lesser extent, melting of land and sea ice (IPCC, 2007a, Chap. 5), and the rate of rise has accelerated in recent decades (Church and White, 2006). Although continued rising sea levels are of significance for many densely populated, low-lying tropical communities adjacent to coral reefs (McGranham et al., 2007), a steady rise in sea level is not considered a major threat to present day coral reefs. Global sea level has been relatively stable for the past several thousand years and some reefs are limited by today's levels and the rates of rise are considered well within the ability of corals to keep up (Smith and Buddemeier, 1992; Done and Jones, 2006).

### Linking the physical environment with biological processes

Determining how coral reefs and associated organisms have and will respond to changing conditions depends upon good observational studies of both the physical environment and biological responses. Ocean climate clearly controls many aspects of coral reef ecosystems but even for the one of the best studied coral reef ecosystems, the Great Barrier Reef, our ability to determine the biotic responses of its many component organisms to climate, climate variation, and climate change is limited. The myriad organisms that make up a tropical coral reef such as microbial assemblages, plankton, macroalgae, seagrass beds, intertidal mangrove, salt marshes and wetlands, benthic invertebrates, sharks and rays, marine mammals, marine reptiles, fishes, and corals are variously sensitive to water characteristics (temperature, chemistry, and

nutrient supply), ocean circulation patterns, and extreme events such as tropical cyclones and freshwater flood plumes (see various chapters in Johnson and Marshall, 2007).

Although we have much better knowledge of the global distribution and health of coral reefs (<http://www.reefbase.org/main.aspx>), it is still difficult to clearly identify a significant increase in coral bleaching events due to confounding factors of greater awareness of the problem and hence more people looking for bleaching events (Oliver et al., 2009). Objective, large-scale methods are necessary for observing, for example, where and when bleaching occurs. These need to be supported by detailed and continuous local-scale observations that track coral reef mortality and recovery from such stress events (Spalding, 2009). It is also important to identify both bleaching-resistant (i.e., reduced impacts despite high thermal stress) and bleaching-resilient (i.e., rapid recovery after stress) coral reefs (McClanahan et al., 2007a). There have been dramatic improvements, through remote sensing, in our capabilities to observe coral reefs across large spatial scales but we still cannot routinely identify bleaching occurrences (Andreou et al., 2004; Elvidge et al., 2004; Mumby et al., 2004). Satellite-based observations since the 1980s have also dramatically improved our ability to detect anomalies in surface ocean climate, and a range of products, based on “oceanic hot-spots” (Goreau and Hayes, 1994), now routinely identify potential bleaching conditions in near real time (Eakin et al., 2009; <http://coralreefwatch.noaa.gov/>). Although such monitoring cannot prevent bleaching, it now allows scientists and reef managers to document the intensity, impacts, and recovery of reefs from such disturbances (see various chapters in Phinney et al., 2006; van Oppen and Lough, 2009).

## Projected future climates for coral reefs

### Predicting future climate

Several factors must be considered to understand and document the potential consequences and impacts of a rapidly changing climate. First, high-quality environmental observations are needed to determine the climatic envelope of particular organisms. Second, we need sufficient understanding of the complex physics of the global climate system, with the various interactions between the atmosphere, ocean, land, cryosphere, and biota, to realistically model current climate. Such GCMs then provide the basis for projecting future changes as a consequence of radiative forcing by greenhouse gases (IPCC, 2007a, Chap. 10). GCMs still, for example, have difficulties in correctly simulating certain components of tropical climate (Neale and Slingo, 2003; Reichler and Kim, 2008). The spatial resolution of GCMs is also relatively coarse which makes projecting to regional scales, most relevant to coral reefs, a challenge (IPCC, 2007a, Chaps. 8 and 11). Third, although based on the same physical laws, different GCMs vary in how they handle (parameterize) key

small-scale processes. This can lead to slightly different results both for present and future climate simulations but such parameterizations are necessary to keep computational costs down to manageable levels. There is, therefore, no single “perfect” GCM and the most recent IPCC-4AR uses multimodel averages of a large number of independent climate projections to account for inter-model variability (Pierce et al., 2009).

Finally, projecting future climates depends on predicting future greenhouse gas concentrations. These depend on a variety of socioeconomic factors that determine the global response and level of commitment to reduce and stabilize greenhouse gas emissions in the atmosphere (mitigation) and, hence, the magnitude and timing of future climate changes. The IPCC constructed a number of plausible scenarios to specify the concentrations of greenhouse gases as input to GCMs (Nakicenovic and Swart, 2000). These range from very carbon-intensive futures with high emission rates (750–800 ppm CO<sub>2</sub> by 2100) to scenarios where emissions are reigned in very quickly (450–500 ppm CO<sub>2</sub> by 2100). Many scientists consider that greenhouse gas reductions well below those of the low emissions scenario are necessary to avoid dangerous climate change (Hansen et al., 2008). We are currently tracking above the high emission scenario (Canadell et al., 2007; Raupach et al., 2007) and, without significant mitigation, we are committed to ongoing, rapid, possibly intensifying climate changes for the foreseeable future, and there is the specter of irreversible changes on the scale of thousands of years (Solomon et al., 2009). Reducing greenhouse gas emissions by 70% by 2100 would, however, halve the magnitude of temperature changes compared to the high emissions scenario and would confine warming of the tropical oceans to 0.5–1.0°C (Washington et al., 2009).

### Projected global changes

Average global temperatures are projected to be ~2–4°C warmer (1.1–6.4°C maximum range from different scenarios) by 2090–2099 compared to 1980–1999 and tropical SSTs are ~1–3°C warmer. An intensified hydrological cycle will increase rainfall in tropical high rainfall regions, reduce rainfall in the subtropics, and the intensity of rainfall extremes will increase. Ocean pH will decrease by 0.1–0.3 pH units. There may be fewer tropical cyclones, but those that do occur are likely to be more intense. It is unclear from global model projections as to what will happen to ENSO events but they are likely to continue as a significant source of interannual climate variability affecting coral reefs (IPCC 2007a, Chap. 10). A conservative estimate is that sea level will rise 20–60 cm by the end of this century, but this value underestimates the contribution of accelerated melting of land ice (Howat et al., 2007; Meier et al., 2007).

### A changing climate for coral reefs: future impacts

Several aspects of the current and ongoing changing climate are of significance for corals reefs, and the environmental

envelope they are used to with warming water temperatures and ocean acidification are likely to be most important (Kleypas et al., 2001; Fabricius et al., 2007; Hoegh-Guldberg et al., 2007; Lough, 2008):

- Warmer waters increasing incidence of coral bleaching and diseases; direct effects on physiological processes of corals and other reef organisms.
- Ocean acidification weakening skeletons and reef structures; direct effects on physiological processes of corals and other reef organisms.
- More intense tropical cyclones increasing incidence of localized reef destruction.
- More intense rainfall and river flow increasing frequency of low salinity waters that extend further offshore, stress corals osmotically, and raise ambient nutrient loadings, producing an environment that favors phytoplankton production, proliferation of macroalgae, increases in filter feeders, and Crown-of-Thorns outbreaks.
- Changed ocean circulation patterns affecting reef connectivity, upwelling, and nutrient supplies.
- Changes to ENSO activity (at present ill-defined) are likely to continue as source of significant interannual climate variability with El Niño events increasing probability of warmer waters throughout most of tropics and, therefore, conditions conducive to coral bleaching and coral diseases superimposed on warmer baseline water temperatures.
- Rising sea level may drown some deeper reefs, increase shallow areas available to others, and wash away low-lying reef islands and cays. Likely to increase destruction associated with more intense tropical cyclones due to higher storm surges and intensified coastal erosion.
- Combined effects of chronic acidification with increased frequency of disturbances to reefs (bleaching, tropical cyclones) and reduced recovery intervals between disturbances.
- Compromising of physical structure of reefs with an overall decline in building of calcium carbonate reef structures, a shift in balance from net calcification to net erosion, and an increased available bare substrate for algae.
- Loss of structural complexity will reduce the range of habitats and shelter available for other reef-associated organisms.

The net effects of this range of increasing chronic and acute stressors associated with a changing climate (combined with, in many locations, already degraded coral ecosystems) are likely to be much simpler and ecologically less complex coral reefs characterized by lower biodiversity. Coral reef “ecosystems” will not respond as a whole (Guinotte et al., 2003) and their regional makeup will change as some species are better able to cope while others become locally extinct (Graham, 2007; Carpenter et al., 2008) and some expand and others contract their current distributions. There will be direct physiological responses by taxa other than corals to

warming waters and ocean acidification. For example, experimental evidence suggests that future temperature and acidification scenarios will lead to reduced fitness and biodiversity losses in coral reef fishes (Munday et al., 2008; Przeslawski et al., 2008).

Several studies have considered aspects, singly and in combination, of these projected climate change impacts on coral reefs. Projections of future SSTs and aragonite saturation state of the Pacific Ocean for the late twenty-first century suggest that nearly all present-day coral reef habitats are likely to be marginal for reef development (though the projected changes are not outside the ranges of current marginal reef habitats). The potential for poleward migration of coral reefs (which depends on temperature, ocean chemistry, and suitable substrate) appears limited (Guinotte et al., 2003). The magnitude of future warming is likely to vary spatially with consequent spatial variability in future bleaching impacts and frequency (Sheppard, 2003; Sheppard and Rioja-Nieto, 2005; McClanahan et al., 2007b). Increases of only 1°C in Caribbean SSTs will expand the extent and intensity of bleaching events to 100% of the area (McWilliams et al., 2005). A similar increase on the Great Barrier Reef (GBR) would increase the occurrence of bleaching from the ~50% observed in 1998 and 2002 to ~80%, with increases of 2–3°C increasing the area of the GBR that bleaches to 97–100% (Berkelmans et al., 2004). Avoiding near-annual coral bleaching events within 30–50 years requires corals increase their thermal tolerance levels by 0.2–1.0°C per decade (Donner et al., 2005), and coral recovery may require management actions that reduce expansion of algae between disturbances (Wooldridge et al., 2005). Modeling studies also suggest that improving water quality through improved agricultural practices can significantly raise the thermal threshold for bleaching (Wooldridge, 2009).

Some studies have also attempted to identify the “tipping point” at which coral reefs can no longer sustain themselves as carbonate structures. Cao and Caldeira (2008) estimate that prior to the Industrial Revolution, 98% of coral reefs lived in waters with suitable carbonate chemistry, whereas once atmospheric CO<sub>2</sub> levels reach 450 ppm, only 8% of reefs will be in waters with the necessary aragonite saturation level. Dramatically, Hoegh-Guldberg et al. (2007, p. 1741) suggest that CO<sub>2</sub> levels greater than 500 ppm combined with water temperatures 2°C warmer will “reduce coral reef ecosystems to crumbling frameworks with few calcareous corals” and similarly that once CO<sub>2</sub> reaches 560 ppm “all coral reefs will cease to grow and start to dissolve” (Silverman et al., 2009, p. 1).

### Combined disturbances and recovery intervals

Long-term observational studies demonstrate the sensitivity of coral reef communities to repeated disturbances. Tropical cyclones, bleaching events, low salinity waters due to heavy rainfall and river flows, outbreaks of



diseases, and coral predators (such as Crown-of-Thorns starfish – see *Acanthaster Planci*) all have direct and flow-on effects to coral reef communities (Wilson et al., 2006; Riegl and Purkis, 2009). Impacts and recovery are variable and repeated disturbances with reduced intervals between them are likely to increasingly compromise the structural integrity and community makeup of these ecosystems (Done et al., 2007; Feary et al., 2007; Wakeford et al., 2008). Because of such multiple climate and local physical stressors on coral reefs, a more holistic modeling approach is required to projecting future status of coral reef ecosystems (Sarmineto et al., 2004).

### Potential actions

Drastic and immediate reductions of anthropogenic greenhouse gas emissions to the atmosphere are the first step to stabilizing global climate and the climatic environment of coral reefs. Coral reefs have been described as one of the “world’s failing ecosystems and one of the most persuasive examples of the effects of global environmental damage” (Downs et al., 2005, p. 486). What other actions, if any, can assist the maintenance of present-day coral reefs into the future? First, protection of these ecosystems from local direct stresses enhances their resilience and recovery from the additional stresses of climate change. This has led to many calls for greatly expanded networks of marine protected areas (Bellwood et al., 2004; Pandolfi et al., 2005; Mora et al., 2006; Wilson et al., 2006; Hughes et al., 2007). At all levels, it is the addition of humans into the equation of coral reefs that is causing the problems (Downs et al., 2005; Mora and Ginsburg, 2008) and it has been argued that we only lack the commitment to implement appropriate protection strategies (Sale, 2008). Second, it is clear that some coral reefs and parts of coral reefs are more resistant to climatic stresses such as bleaching and some are more resilient as demonstrated by relatively rapid recovery. Such reefs and locations within reefs are clear targets for enhanced protection (West and Salm, 2003; McClanahan et al., 2007a; Graham et al., 2007, 2008; Diaz-Pulido et al., 2009). Third, climate change and increased likelihood of significant disturbances need to be incorporated into selecting, designing, and managing marine protected areas (Baker et al., 2008; Game et al., 2008). Fourth, we need to improve early warning systems, seasonal climatic outlooks, and monitoring of physical and biological conditions on reefs (Weeks et al., 2008; Maynard et al., 2009; Spillman and Alves, 2009). Finally, we need improved GCMs for the tropics (Shukla et al., 2009) including better spatial resolution to allow better and more reliable predictions to be made for specific reef provinces (Donner et al., 2005, 2009).

### Summary

Coral reef ecosystems are highly vulnerable to stresses associated with a changing climate. These stresses are superimposed on local stresses in many regions that have

already resulted in significant degradation in the goods and services that healthy coral reefs provide (Buddemeier et al., 2004). Coral reefs are unlikely to disappear, but in the future they are likely to calcify less and there will be fewer reefs that are able to sustain the necessary reef framework that supports many thousands of marine organisms with a consequent loss in marine biodiversity (Guinotte et al., 2003). Our understanding of the full consequences of a rapidly changing climate and ocean chemistry for coral reef ecosystems is still limited and, unfortunately, the experiment is occurring in real time in the real world. The consequences of anthropogenic climate change for coral reefs are inequitable. The countries most responsible for anthropogenic climate change produce 6–11 times more CO<sub>2</sub> per person than the more than 400 million people living close to coral reefs (Donner and Potere, 2007). It is, however, these communities that will suffer most from the loss of the goods and services provided by healthy coral reef ecosystems.

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## Cross-references

[Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity](#)  
[Climate Change: Increasing Storm Activity](#)  
[Corals: Environmental Controls on Growth](#)  
[El Niño, La Niña, and ENSO](#)  
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[Tropical Cyclone/Hurricane](#)  
[Zooxanthellae](#)

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## CLIMATE CHANGE: IMPACT OF SEA LEVEL RISE ON REEF FLAT ZONATION AND PRODUCTIVITY

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### Definitions

**Climate change:** projected changes to atmosphere and ocean which may affect coral reefs and their biota in a detrimental way, usually considered over the next 100 years or so.

**Sea level rise:** one of these projected changes resulting initially from thermal expansion of the oceans and longer term melting of glaciers, projected to be 13–68 cm by 2100.

**Reef flat:** the intertidal part of the coral reef, exposed at low tide, often sediment covered but with living corals in pools, for example as micro atolls, or around the lower edges of the reef flat where exposure is of shorter duration.

**Productivity:** the production of calcium carbonate forming the framework and sediments of the reef. Usually expressed as kilograms per square metre per year ( $\text{kg m}^{-2}/\text{year}$ ), the figure may be converted into reef accretion rates by taking into account the density and porosity of the contributing organisms and detrital facies.

### Introduction

The impact of sea level rise on coral reef flats was one of the first considerations raised in relation to climate change and coral reefs. Most publications in the 1980s considered the impact to be a beneficial one. This was especially so in the Indo-Pacific area, where isostatic adjustments had produced a sea level at or above its present position for over 6,000 years. Many reefs are now adjusted to this level with lagoons infilled, sediments dominating the reef flat and living corals limited to shallow pools (Figure 1). Such reef flats are too shallow for at least half the tidal cycle for the transmission of waves with sufficient energy to entrain and transport all but the finest sediments.

Many general references on Greenhouse effects emphasized the rejuvenation of reef tops (e.g., Henderson-Sellers and Blong, 1989) whilst others went as far as suggesting reefs could be drowned and many ecosystems eliminated (e.g., Falk and Brownlow, 1989). Some scientific assessments suggested that renewed coral growth would make reef flats aesthetically more pleasing (e.g., Hopley and Kinsey, 1988).

### Reef flat attributes and sea level rise

Atlantic reefs have experienced a continuous sea level rise throughout the Holocene (for isostatic reasons) with the result that their shallowest points are commonly subtidal and have a living coral cover. They are thus well placed to accelerate their growth as sea level rises. Indo-Pacific reefs, however, already at sea level for over 6,000 years, are very different. Many lagoons have been completely infilled (see *Reef Classification by Hopley (1982)*). Rather than living corals, shingle ridges and cemented platforms are to be found on the windward margins of many reefs and mangroves have colonized the sheltered areas behind them. The result is the typical low wooded island morphology found, for example, on the northern Great Barrier Reef (GBR). Reef flats are sediment covered often stabilized by binding organisms such as seagrass and macro algae. Corals, including micro atolls may be confined to moated parts of the reef flat.

Geomorphologically, these reef flats are inert for much of the time. As demonstrated by Kench and Brander (2006), at Warraber Island in Torres Strait (maximum tidal range ca. 4 m), Lady Elliott Island, in the southern GBR (1.7 m) and Cocos-Keeling atoll in the Indian Ocean, (1.2 m), both the high loss of energy of incident waves at





**Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity, Figure 1** Inert reef flat which has been at sea level for >5,000 years. Coconut (Poruma), Torres Strait.

the reef edge and long subaerial isolation at low tides are the reasons for their being insufficient energy for sediment movement. The Warraber reef flat is inactive for long periods, with waves above 0.05 m on the outer reef flat <30% of the time and 0.1 m only 19% of the time on each Spring to Neap cycle. “Energy windows”, when waves can perform geomorphic work, are determined by critical water depths which are exceeded between 16.2 and 38% of the time at the GBR sites. However, on Cocos-Keeling because it is open to oceanic swells and has a low tidal range, this time period can be up to 76% of the time, thus accommodating greater sediment movement.

### Reef flat response to sea level rise

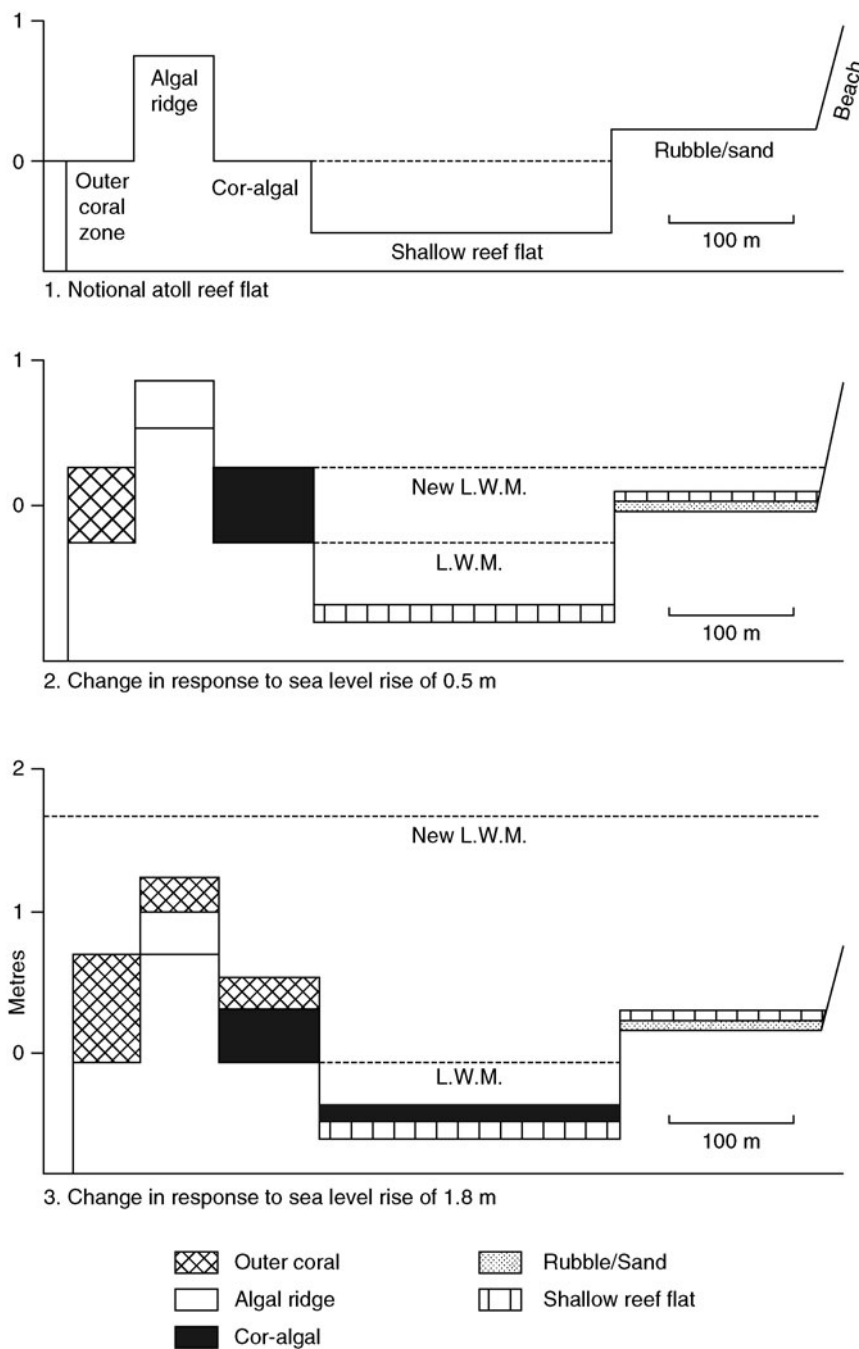
Analyses of different scenarios of rates of sea level rise on the typical zones of reef flats and reef islands have been made by Hopley and Kinsey (1988); Hopley (1993); Hopley (1997); Hopley et al. (2007). Projections for 2100 by Hopley and Kinsey (1988) were up to 1.8 m, but by 1993, they were a more modest 30 cm to 1.0 m (average 60 cm), by 1997 23–96 cm and currently 13–68 cm (all figures from IPCC reports). Although the rate of annual sea level rise ranges from only 5 to 15 mm/year, this is important for reef flat ecology because it approximates the vertical growth rates of some of the slower growing corals. The realized value of sea-level rise will determine how much and how quickly vertical accommodation space is added, the places and heights that corals may grow, and the wave energy, currents and hence sediment transport on the reef flat (see *Accommodation Space*). Response in the form of vertical accretion can also be calculated. Estimates using alkalinity anomaly measurements (Kinsey, 1985), closely match those from the

geological record (Davies and Hopley, 1983). For the major ecological zones these vertical accretion rates are:

- 100% coral on hard substrates – modal rate of 7–8 mm/year but up to 15 mm/year for highly porous branching corals on a hard substrate.
- Algal pavement – 3–4 mm/year
- Reef flat sand and rubble – 0.4 mm/year

Using these figures Hopley and Kinsey (1988) suggested that reef flats would be completely rejuvenated in 100–150 years accreting initially at 4 mm/year then accelerating to 7 mm/year. Reef growth rates from dated cores indicate that all reefs would be drowned by a sea level rise >8–9 mm/year. For many inshore reefs of the GBR, rejuvenation would be aided by inundation of 1–1.5 m raised reef substrate dating from higher sea level stands of the mid-Holocene times.

By the mid-1990s sea level rise projections were more conservative (0.3–1.0 m, average 60 cm). Hopley (1997) modeled the impact of both the earlier rise of 1.8 m and a more modest 0.5 m on a typical atoll reef flat (from Bikini, Emery et al., 1954) (Figure 2). The higher rise resulted in the inundation of the entire reef flat by about 2070, the outer flat becoming entirely coral covered, producing sediment for the deepening lagoon and inner sand/rubble flat as wave transport became more efficient. In contrast the response to the slower rate of rise was a reef flat that more or less retained its original zonation. The inner flat may become shallowly submerged but even here transport of sediment from the windward margin may maintain its level at about LWM. Calculating the calcium carbonate production for a 1 m wide transect across the entire 70 m wide atoll reef flat produced a figure of 2,020 kg/year for the present time, and a similar



**Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity, Figure 2** Modeled atoll reef flat and response to a sea level rise of 0.5 and 1.8 m by, 2100 (from Hopley, 1997).

2,220 kg/year for the similar zonation in 2100 after a 0.5 m rise. After a rise of 1.8 m, by contrast (Figure 2), the carbonate production rate across the reef flat was 4,950 kg/year and the reef flat zonation highly modified with much of the active coral growth having moved shorewards.

Hopley et al. (2007) also undertook a similar exercise for a >3 km wide reef top typical of some GBR planar

reefs. Again, calcium carbonate productivity was increased only marginally by a rise in sea level of 0.5 m. However it was more than doubled by the larger rise as the reef top was rejuvenated. In both instances water levels would rise over the reef flat, laterally transporting much of the new material towards leeward cays, or lagoons. This would be especially so if a large proportion of the new growth

was in the form of fragile branching corals, small foraminifera or other easily transportable sediment components.

Some efficiency in sediment movement may be lost as the new reef top becomes rougher with new vertical relief in the form of coral spurs, storm rubble, etc. (Kench and Brander, 2006). Generally shallow lagoons are likely once more to become effective sediment sinks. In some circumstances, there may be a surplus that can contribute to island construction.

### Reef island responses

Initial climate change predictions described dire consequences for reef islands, as contours representing extreme high tide level were merely moved upward on island shores. However, researchers working directly on the physical processes on reefs (see Hopley et al., 2007 for discussion) generally agree that rising sea levels of the magnitude projected over the next 100 years will be far less damaging and will produce substantial reworking of surficial sediments enough to at least maintain the island mass. Island stability will be aided by a retaining effect of beach rock and other cemented materials. Additional transported sediments and higher water levels will allow cyclonic storms to more effectively emplace shingle ridges to motus, a very important part of the island building processes (e.g., Bayliss-Smith, 1988; Maragos et al., 1973). Sediment movement will also occur on a more regular basis. Kench and Brander's (2006) research on mesotidal Australian reefs indicated that sediment movement is currently restricted to less than 50% of the time. On Warraber Reef in Torres Strait (and other Indo-Pacific reefs) effective sediment movement ceased about 2,000 years ago but a rise in sea level of only 0.5 m may unlock stored sediments which will be moved towards an adjacent cay or motu.

Similar responses have been modeled on Raine Island (northern GBR) by Gourlay and Hacker (1996). They indicated that the height of the beach berm is determined by the run-up height of the dominant wave action – at highest Spring Tide. A berm elevation of 4 m could be built by small flat waves of 0.5 m height breaking directly onto a beach at a tide level as low as 2.3 m. They showed that a small rise in sea level without any corresponding build up of reef flat level would result in the attainment of greater berm height under most weather conditions, i.e., build-up of the island by an amount which would exceed the amount of increase in water level. On Raine Island they suggest that with a 0.6 m rise in sea level, larger 1.6 m waves would increase berm height by a factor of 0.8 m. Smaller waves of 0.5 m would increase the height by 1.2 m, i.e., berm height would increase from an initial 4.0 m to up to 5.2 m.

Whilst the island mass may remain as a habitat for plants and animals it will be highly disturbed. Deposition on one part of the shore will be matched by erosion elsewhere as both prevailing wind directions and storm frequencies add to the impacts of sea level rise. Reworking of older parts of the island may remove a high proportion

of the mature organic soils and vegetation which form the most favorable habitat including as agricultural land for human populations. For migratory species such as seabirds and turtles, the reworked island may for a time, still provide a valuable resource but for permanent residents, coral reef cays may quickly become uninhabitable.

### Other factors influencing reef flat change

The start of this entry presented the optimistic view that coral reefs may be one of the few ecosystems to benefit from sea level rise. The discussion that followed suggested the optimism may be well founded in the light of renewed upward growth, changed wave action and increased sediment movement. However, sea level rise is not the only factor in climate change. Whilst increased cyclone activity may help add new ridges to reef islands, other environmental changes such as temperature rise and ocean acidification will have detrimental affects resulting in widespread coral mortality.

Sheppard et al. (2005) have described the results of coral bleaching in reefs of the Seychelles. Prior to the 1998 event fringing reefs had an outer veneer of 0.5 m high thickets of staghorn corals and massive *Porites*. Stripping of this veneer reduced reef roughness and created a pseudo sea level rise that was superimposed over a regional rise of ca. 5 mm/year. Sheppard et al. modeled the reef flat conditions of 1994, 2004 and 2014 concluding that the rate of erosion of Seychelles beaches would double in the next 10 years.

These figures are of great concern for many of the world's reefs subjected to rising sea level. However, reef disintegration as described for the Seychelles may not be nearly as rapid elsewhere, determined largely by the composition of the reef flat corals. Reef flat surfaces subject to a small fall in sea level remain within the energetic wave zone as well as the intertidal zone of highly active bioerosion. Where branching corals dominate the reef flat, stripping and pseudo-sea level rise may impact on the adjacent shore, as in the Seychelles. However, where massive or encrusting corals are dominant even though they may die in response to environmental change, they may not be removed, but stay *in situ* on the reef flat for 5,000 years or more, as illustrated by Hayman Island in the central GBR (Kan et al. 1997). Here a pseudo sea level rise is not superimposed on regional sea level behavior.

### Summary

Responses of reef flats to sea level rise in the twenty-first century will likely be many and varied. The response in each case will depend on specific reef characteristics and environmental setting: the existing height of the reef relative to sea level; the local tidal range and rate of sea-level rise; the existing composition and zonation of coral assemblages, and hence susceptibility to the exacerbating effect of pseudo sea-level rise; the changing ecology with changed environmental conditions and disturbance regimes; and propensity for old and new sediments to be transported by wave action.



The only generalization is that the response of coral reefs will not be the same in all locations.

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## Cross-references

[Accommodation Space](#)  
[Climate Change: Impact On Coral Reef Coasts](#)  
[Climate Change and Coral Reefs](#)  
[Geomorphic Zonation](#)  
[Hydrodynamics of Coral Reef Systems](#)  
[Recent Sea Level Trends](#)  
[Reef Flats](#)  
[Sediment Dynamics](#)

## CLIMATE CHANGE: IMPACT ON CORAL REEF COASTS

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### Definition

Climate change is impacting directly on coral reef coasts. When warm spikes, superimposed on a long-term gradual warming trend, cause massive mortality of corals, the elevation of the shallow reef relative to the shore is lowered, thereby increasing the wave energy that reaches the shore and the consequent erosion of low lying shores.

### Introduction

A primary service supplied by coral reefs to the human communities which live near them is that of shoreline protection. Infrastructure and settlements occur along the shorelines of many hundreds of atolls, as well as along thousands of kilometers of shoreline of high islands. They are all protected to a considerable extent by the breakwater effect provided by coral reefs that fringe those shores. The reef's service in this respect is invaluable, but quantification of the effects and costs caused by their degradation lags well behind many of the better studied biological effects. Much of what we do know derives from engineering models.

The main impacts are caused by increases in the amount of wave energy which strikes the shoreline when the adjacent reef deteriorates, and when its elevation drops relative to sea level. In the recent past, this form of deterioration has come mainly from coral extraction to obtain limestone for building purposes, and from coral mortality caused by diseases. Now, and in the foreseeable future, it will be compounded by effects of global warming.

Traditional extraction of corals for use as building material, both as whole colonies or as excavated blocks of reef, has occurred for centuries. Perhaps the best known example of this has taken place in the Maldives, where the lack until recently of any significant quantity of alternative building material has meant that the reef flats around several settlements, especially the capital Malé, have been severely excavated. There are no good estimates of quantities taken, but it seems likely that around Malé the reef flat appears to have been excavated by local people to such an extent that they have lowered its elevation relative to sea level by at least half a meter.

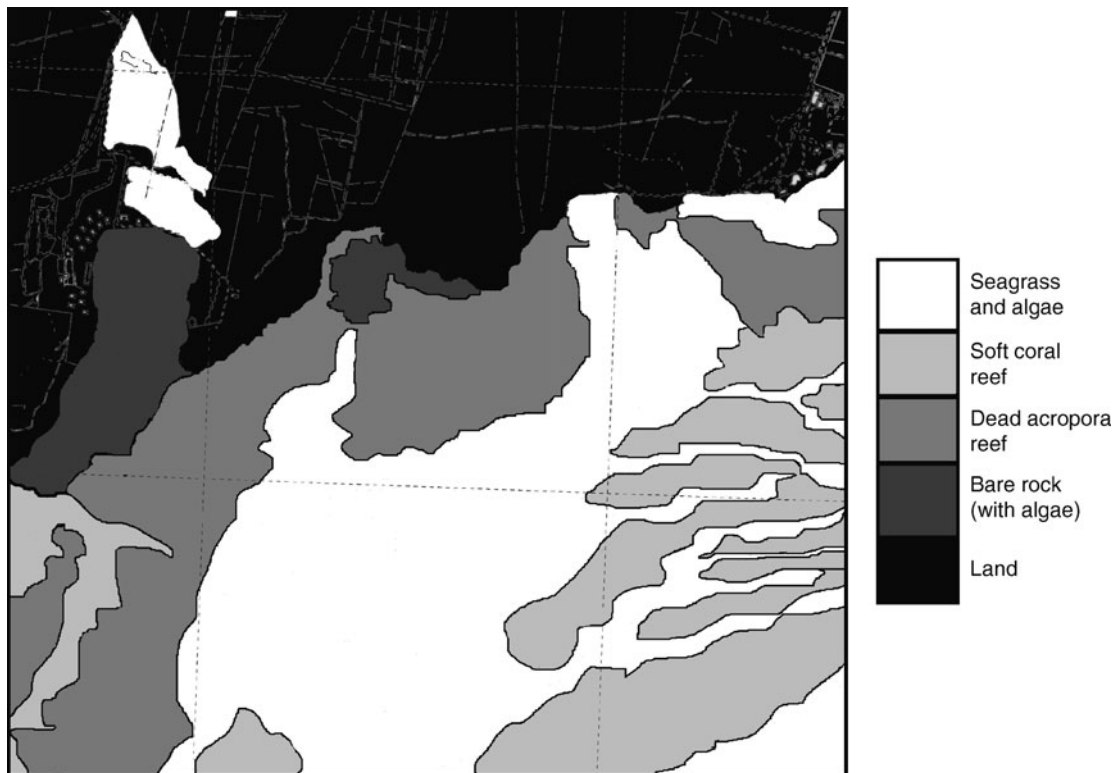
Coral mortality from disease has especially affected the elevation of reef crests in the Caribbean. Until the 1980s the shallowest zone of corals comprised Elkhorn coral, *Acropora palmata* (Geister, 1977). This species grows upward to reach the low water mark in very dense thickets of over 2 m tall, even protruding above the water at low tides. However, over much of the Caribbean, these shallow water reefs have now disintegrated almost completely.

Enormous stands of very solid limestone colonies that packed the zone from the surface to about 4 m depth have been almost totally eliminated by disease (Rosenberg and Loya, 2004). As a result, affected reefs no longer contain a wave break reaching the low water level. Instead, this zone now consists of disintegrating rubble, remnants of the once-living branching coral, with a completely different ecological character. The areas are extensive: Figure 1 is an example from the island of Anguilla, where the extensive shallow, dead reef was previously a healthy *Acropora palmata* zone.

Sea water warming – the third cause of wide-scale erosion of coral reefs – is increasing in importance. Warm spikes, superimposed on a long-term gradual warming trend, have caused massive mortality of corals in many parts of the world. In the context of shoreline protection, the significant mortality is that of the very shallow corals on reef crests and reef flats. It results in a drop in the elevation of the corals, followed by a corresponding drop in the ability of the reef to absorb wave energy, and a consequent increase in the amount of wave energy that reaches the shore.

### Quantification of the problem: a case study

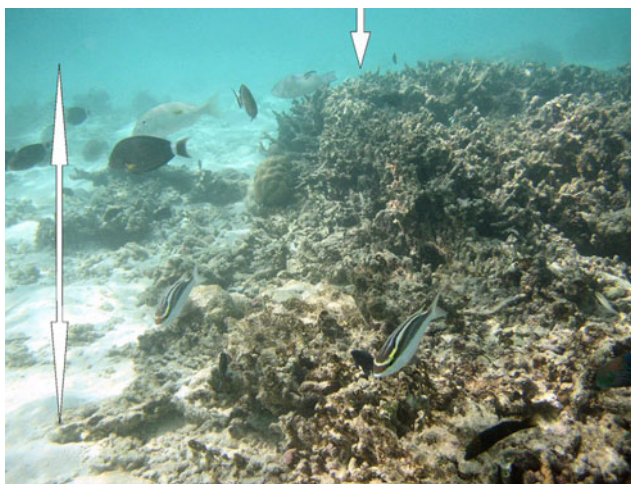
The effectiveness of the “breakwater” role of reefs is well known in general principle and assumed to be substantial, but has been poorly measured and is difficult to predict. However an example from the Seychelles (Sheppard et al., 2005) has estimated approximate magnitudes. There, concern was expressed about several areas of apparently increased shoreline erosion as well as a smaller number of areas where substantial pulses of sand had been pushed onshore over coastal roads. In 1998, warming in the central granitic islands had caused substantial coral mortality which was not recovering to any significant degree; indeed the reefs appeared to be slowly disintegrating. Prior to the late 1990s, the fringing reefs around the granitic islands had supported a complex ecology, including rich growths of corals. Luxuriant reef flats extended seaward from the sandy coasts of the islands to the reef face, or drop-off. These reef flats supported dense stands of corals (along with patches of seagrass, sand, and rubble) which grew up from the reef flats to the surface of the water at low tide (Figure 2). The horizontal, solid platform of the reef flat on which these corals grew is located



**Climate Change: Impact On Coral Reef Coasts, Figure 1** Simplified section of a Geographical Information System map of Anguilla, Eastern Caribbean, showing distribution of dead Elkhorn reef. Map is approximately 500 m<sup>2</sup>. The *mid gray color* (see key) was probably all Elkhorn before being killed before the 1980s. Further, the darkest gray (bare rock with algae) may also have been Elkhorn but has decayed through erosion sufficiently so as not to be recognisable as such. *Pale gray* is reef dominated by soft corals (*Gorgonacea*) but with some limited quantities of the reef building *Montastraea* coral. White is various mixtures of seagrass and sandy substrate with some seagrass.



**Climate Change: Impact On Coral Reef Coasts,**  
**Figure 2** Fringing reef of Praslin Island, Seychelles. Reef flat is 205 m wide, on calm day with small waves breaking at the edge of the reef flat. Dark patches underwater are seagrasses to shoreward and dead coral further seaward.



**Climate Change: Impact On Coral Reef Coasts,**  
**Figure 3** Underwater photograph (2004) of the profile of one of the reefs (off the main island), showing *Acropora* stand which had been dead for about 6 years and which has been progressively disintegrating. Top arrow represents distance between low water and the top of the reducing coral stand, lower arrow represents the distance between the 2004 upper surface of the coral stand and the plane of the reef flat.

generally 1–2 m below low tide. Typically, perhaps half of any single reef flat was covered by tall branching corals which, by the early 2000s, were dead and slowly disintegrating (Figure 3), with the result that the upper surface of the coral stands was eroding and dropping relative to sea level (Figure 4).

Wave set up, transformation, and propagation to the shore on coral reefs have been researched by Gourlay

and colleagues (Gourlay, 1994, 1996a, b, 1997; Gourlay and Colleter, 2005; Massel and Gourlay, 2000), based on both laboratory experiments and field measurements (Hardy et al., 1990; Hardy and Young, 1996). Important factors include the width of the reef flat; the proportion of the reef flat covered by corals; the depth in calm water conditions of both the tops of the coral stands and their base relative to the platform and sea level; and the height of the coral stand (pre- and post-mortality and collapse). Equations can be derived to predict the wave-forced, raised water level on reef flats resulting from wave breaking. This in turn depends on offshore wave height and period, and the decay of energy from reef edge to shoreline. Sea level rise may be factored in, as well as rounding and smoothing of the reef crest and reef flat as corals die and disintegrate.

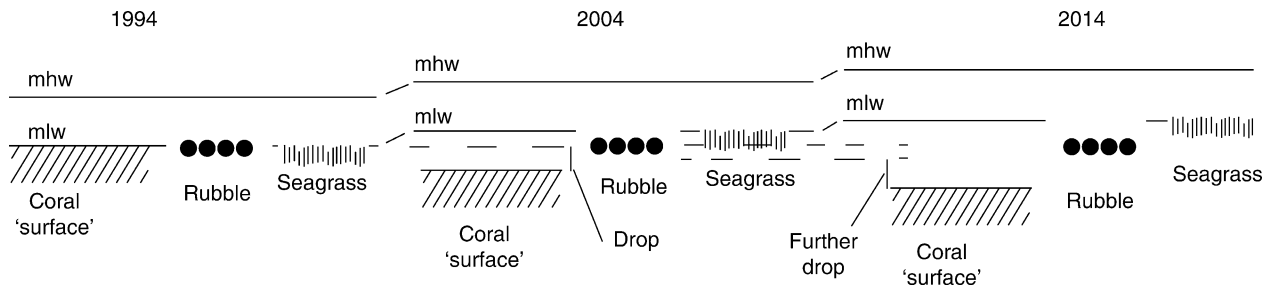
In the Seychelles study it was found that the main driver of change in wave energy reaching shores was the “pseudo-sea level rise” created by increased depth resulting from disintegration of coral colonies. An additional factor was a reduction in rugosity as irregular and rough coral colonies slowly became converted to a smoother plane. Also taken into account was the proportion of each section of reef flat that was covered by corals (areas covered by seagrass or sand were treated differently by assuming either no change or by assuming that seagrass beds can grow vertically in response to changing water levels). In a before and after comparison (all coral stands reaching the low water surface compared to complete disintegration of the corals) the reduced roughness and greater depth resulted in much greater wave energy reaching the shore (Figure 5). Mitigating against the rising energy reaching the shore to some degree was coral mortality at the reef crest. Disintegration of these corals rounded off the reef in that area, affecting the initial wave set-up, in some cases changing reef morphology so that formerly distinctive reef flat, crest, and slope became blended together over a near-indistinguishable boundary. Reef flats with partial disintegration of previously abundant corals permitted about 20–60% more energy to strike the shoreline, whereas total disintegration permitted an additional 75% energy. An average 7–8% reached the shore before the mass coral mortality, about 11% in 2004, and a predicted 18% will reach the shore when coral attrition is complete. The sequence of events included an initial pulse of sand being created as corals initially died (in 1998), after which it, and the sand on the beach, was removed in an extended erosion phase.

There appear to be no quantitative data for other shoreline areas protected by coral reefs, though the effect is becoming commonplace, with shoreline attrition, especially on many coral atolls, being meters or tens of meters (Figure 6).

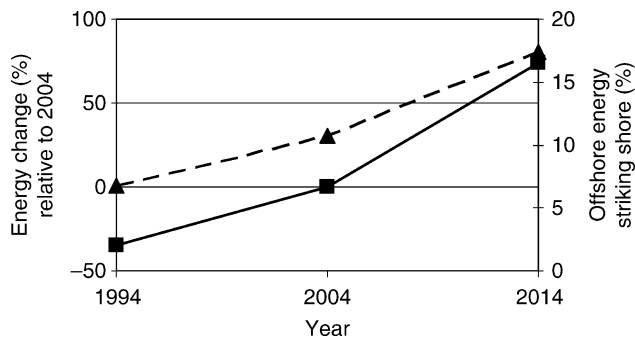
## Summary

A case study conducted in the Seychelles is described, in which it was estimated that the demise of the shallow





**Climate Change: Impact On Coral Reef Coasts, Figure 4** Sketch of measured parameters at the three stages, from left to right: a decade ago, today, and a decade in the future. Note that coral surface drops each decade, while seagrass keeps pace with sea level rise. Bare rock (not shown) remains unchanged in elevation throughout. (From Sheppard et al., 2005.)



**Climate Change: Impact On Coral Reef Coasts, Figure 5** Graphs of wave energy reaching shore (average of 14 reefs). Left: Y axis and solid line is change in energy (%) relative to the year of observation. Right: Y axis and dashed line shows percent of offshore energy reaching shore at the three time intervals.



**Climate Change: Impact On Coral Reef Coasts, Figure 6** Example of recent shoreline erosion on a coral atoll (Chagos archipelago, Indian Ocean). The dead palm trees are now in the low intertidal zone and show that the land extended considerably to the left of their position - in fact to the exposed ridge on the left of the photo. Horizontal land loss here has been 20–30 m. (Photo Anne Sheppard.)

corals has and will result in an approximate doubling of wave energy striking the previously protected shorelines. This has resulted in substantial erosion with a high cost to the local population.

There are many anecdotal stories of shoreline erosion from around the world, especially around atolls. It is likely that a proportion of them are exaggerated or that the observations made are merely reflecting seasonal changes; it is well known that sandy shorelines behind coral reefs can change by tens of meters or even more on a seasonal basis. However, it is usually not too difficult to distinguish between seasonal changes and unidirectional or progressive changes that have progressed for several years, if only because the latter soon begins to show erosion of previously stable and long-lived shoreline vegetation (Figure 6), and then erosion of built infrastructure. Nevertheless the poor signal-to-noise ratio in matters of shoreline movement is a serious problem, making it difficult, in some cases, to distinguish between the seasonal and storm-driven noise in the system and any underlying, serious progressive trend that may be occurring. What is clear is that all forms of coral damage, whether from local, direct impacts, or from climate change, will reduce the effectiveness of the break-water effect provided by living coral reefs. Furthermore, in some cases, changes seen to date will be very much less than those predicted for the near future if temperatures continue to rise and if polluting discharges and mechanical extraction continue to reduce the abundance and resilience of coral reefs that fringe shorelines.

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## Cross-references

[Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity](#)  
[Climate Change: Increasing Storm Activity](#)  
[Climate Change and Coral Reefs](#)  
[Engineering On Coral Reefs With Emphasis On Pacific Reefs](#)  
[Indian Ocean Reefs](#)  
[Reef Flats](#)  
[Reef Front Wave Energy](#)  
[Sea Level Change and Its Effect on Reef Growth](#)

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## CLIMATE CHANGE: INCREASING STORM ACTIVITY

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## Synonyms

Increasing ecological disturbance; Increasing tropical cyclone (hurricane, typhoon) frequency and intensity

## Definition

An increase in the intensity and/or frequency of storms relative to a predefined expectation (e.g., historic yearly average or quantile).

## Introduction

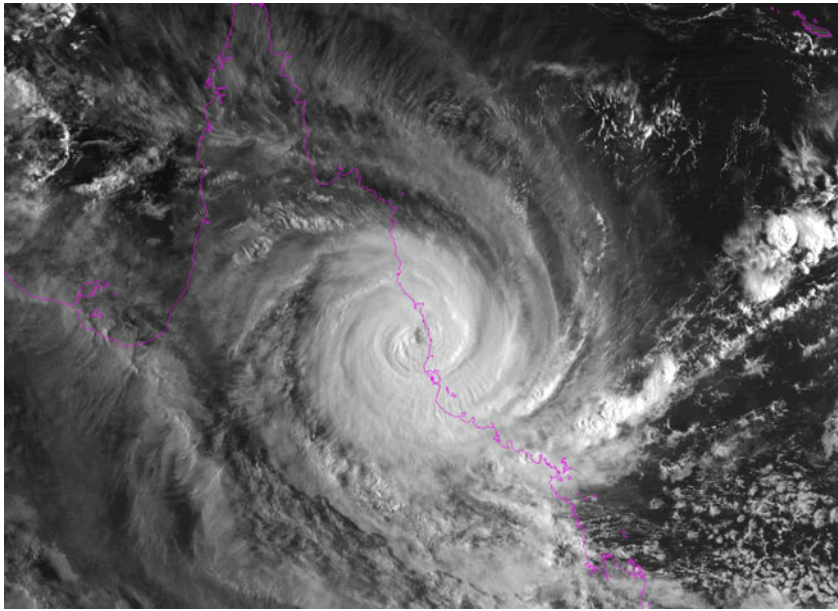
Increasing storm activity is a hypothesized consequence of climate change that results predominantly from warming sea surface temperatures (SST). Significant scientific debate revolves around whether or not the storm activity is increasing and, if so, whether any increases are a consequence of global warming. This debate exists primarily because detecting such trends depends on the temporal and spatial scales examined, the duration and quality of available meteorological records, and the kinds of statistical and mathematical approaches used in analyses. Storms temporarily alter the physical state of coral reefs in a number of direct and indirect ways (see [Tropical Cyclone/Hurricane](#)). Direct examples include changes in

salinity (via rainfall) and impinging wave climate (via wind). Indirect examples include increased terrestrial runoff and associated changes in turbidity, chemistry, and human-induced pollution levels. By altering the physical state of ecological communities, storms are an important form of ecological disturbance that significantly shape ecological systems and are hypothesized to be at least partially responsible for the levels of species diversity. Increasing storm activity will drive changes in the biological and physical structure of coral reefs, and in turn the ecology of organisms that rely on the reef habitat for shelter. Although some studies have forged mechanistic links between storm activity and coral reef vulnerability, the impacts of increasing storm activity on coral reef ecology and physical structure of reefs remain largely unknown ([Figure 1](#)).

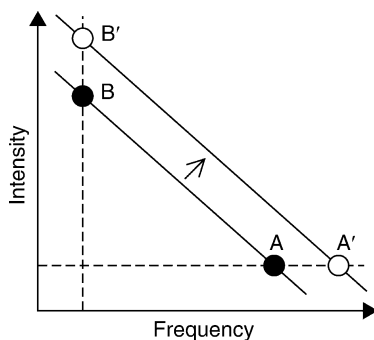
## Evidence

Theory suggests that tropical storm activity should increase with global mean temperature as warmer seas fuel tropical storm generation (Emanuel, 1991). While growing evidence strongly suggests that SST is increasing in tropical seas (see [Temperature Change: Bleaching](#)), evidence for increasing storm activity is less clear cut. Part of the reason for this uncertainty is that storm activity is comprised of two components that must be considered simultaneously: storm intensity and storm frequency ([Figure 2](#)). In general, more intense storms are less frequent (e.g., yearly cyclones) and less intense storms are more frequent (e.g., daily to weekly squalls). An increase in storm activity would theoretically shift this relationship upward (illustrated by the arrow in [Figure 2](#)). Such a shift can be interpreted in two ways. First, storms of a given intensity would increase in frequency within a given time period (A to A', [Figure 2](#); e.g., an increase in the number of category 3 cyclones each year). Second, storms of a given frequency would increase in intensity (B to B', [Figure 2](#); e.g., the largest yearly storm is more intense on average).

Early attempts to detect changes in storm activity focused on frequency and uncovered no clear trends. In fact, a more recent modeling effort suggests that Atlantic tropical storm frequencies might even decrease under future greenhouse-gas-induced warming (Knutson et al., 2008). Despite possible decreases in storm frequencies, studies (including Knutson et al., 2008) have shown that storm intensity is increasing. For instance, Emanuel (2005) looked at storm power dissipation (a measure of the total energy generated by a storm) and found it to be highly correlated with temperature, reflecting global warming. These results appear paradoxical according to [Figure 2](#): how can tropical storm intensity increase but yearly frequency decrease or stay unchanged? The answer becomes apparent when looking at the distributions and extremes of yearly storm intensities rather than averages (Gaines and Denny, 1993). In a study looking at the maximum wind speeds generated by tropical cyclones, Elsner



**Climate Change: Increasing Storm Activity, Figure 1** Cyclone Larry crosses the Great Barrier Reef, Australia, in 2006 (MTSAT-1R: Satellite image originally processed by the Bureau of Meteorology from the geostationary satellite MTSAT-1R operated by the Japan Meteorological Agency).



**Climate Change: Increasing Storm Activity, Figure 2** A schematic of the general inverse relationship (*bottom solid line*) between storm intensity and frequency, the two components of storm activity. Increasing storm activity would result in the relationship moving outwards (*top solid line*). See text for details.

et al. (2008) show that, while there is no trend in frequency nor the average maximum wind speed of yearly cyclones, the upper quantiles of maximum wind speeds indeed increase from year to year. That is, in each year a similar number of tropical storms reach “cyclonic” status and the maximum wind speeds generated by storms are similar on average; however, the maximum winds speeds of the largest storms are increasing. Simulations by Knutson and Robert (2004) support this idea, finding that warming induced by greenhouse gas entrapment may lead to increasing occurrence of highly destructive category 5 storms. Furthermore, Hoyos et al. (2006) link the increasing trend in number of category 4 and 5 hurricanes for the

period 1970–2004 directly to the trend in sea surface temperatures. However, Emanuel et al. (2008) concludes in a reanalysis of data from his 2005 study that the increase in power dissipation in recent decades cannot be completely attributed to global warming.

In summary, despite the growing evidence that the distribution of tropical storm intensities per year has stretched upward, the link between increasing storm activity and global warming remains unclear. The World Meteorological Organization (2006) state in a press release that “though there is evidence both for and against the existence of a detectable anthropogenic signal in the tropical cyclone climate record to date, no firm conclusion can be made on this point” and that “no individual tropical cyclone can be directly attributed to climate change.”

### Conclusions: consequences for coral reefs

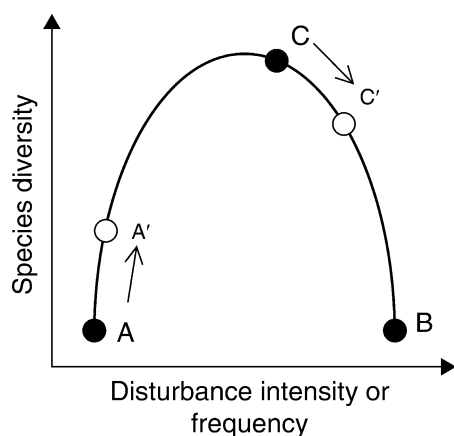
Storms have a number of direct and indirect effects on coral reefs. Direct effects include mechanical damage and sedimentation to corals and reef structures by waves, storm surges, and currents, as well as lowered salinity by torrential rainfall (Woodley et al., 1981; Massel and Done, 1993; Madin and Connolly, 2006; Fabricius et al., 2008). Indirect effects include pollution and sedimentation caused by terrestrial runoff (Fabricius, 2005). Storms also have sub-lethal effects on the reef-building corals, such as physiological stresses that can lead to decreased growth, competitive ability, and reproduction as well as increased susceptibility to disease and bleaching.

One way to conceptually illustrate the influence of increasing storm activity on coral reef biodiversity is via



the Intermediate Disturbance Hypothesis (IDH; Connell, 1978). According to this hypothesis, a patch of reef that is exposed to mild and/or infrequent disturbances is likely to become dominated by one or a few species (the stronger competitors), resulting in low species diversity (point A in Figure 3) because these low-level storms rarely remove the dominant corals to create an empty space for new species to settle. On the other hand, very few species are able to survive extreme and/or frequent disturbance events, such as unusually high wave forces, bombardment and scouring by waterborne objects, and/or lowered salinity, also resulting in low species diversity (point B, Figure 3). As a result, species diversity tends to be highest on average at some intermediate disturbance level (e.g., near point C, Figure 3).

Assuming that the IDH provides a reasonable approximation for the relationship between the storm-induced disturbances and coral diversity, then increasing storm activity will affect the diversity of different reefs in different ways. For example, diversity might be expected to *increase* in benign reef patches that currently have low levels of diversity due to recent history of low disturbance (A to A', Figure 3). Conversely, diversity is expected to *decrease* on those portions of reef patches that currently have high diversity due to a recent history of intermediate disturbance (C to C', Figure 3). In order to make predictions about how reefs might change if storm activity were to increase, Madin et al. (2008) use an engineering model to measure the mechanical vulnerability of different colony shapes to storms. They show that, if storm activity increases and/or ocean acidification weakens carbonate structure (see *Ocean Acidification, Effects on Calcification*), future reefs will have fewer corals and be dominated by small and simple forms, which will in turn support lower levels of whole-reef biodiversity than do present-day reefs.



**Climate Change: Increasing Storm Activity, Figure 3** A schematic representation of the Intermediate Disturbance Hypothesis. See text for details.

In summary, even through the use of a simple model (the IDH), it becomes clear that the influence of increasing storm activity on coral reef systems is likely to be complex and dependent on many factors, including history (e.g., past disturbance regimes; see *Historical Ecology of Coral Reefs*), plant and animal biology and biomechanics, dispersal to other reefs, growth plasticity (responsiveness to the environment), and, if changes are sufficiently gradual, adaptation (generational shifts in characteristics that improve survival; see *Adaptation*).

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## Cross-references

[Adaptation](#)  
[Climate Change and Coral Reefs](#)  
[Ecomorphology](#)  
[Historical Ecology of Coral Reefs](#)  
[Ocean Acidification, Effects on Calcification](#)  
[Temperature Change: Bleaching](#)  
[Tropical Cyclone/Hurricane](#)  
[Waves and Wave-Driven Currents](#)

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## COCOS (KEELING) ISLANDS

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### Definition

The Cocos (Keeling) Islands are a remote group of islands, forming a single horseshoe-shaped atoll and an isolated island, North Keeling, in the eastern Indian Ocean. They represent the only atoll that Charles Darwin visited and became central to his theory of coral reef development, and have played a central role in several subsequent debates about reef development in relation to sea level.

### Introduction

The Cocos (Keeling) Islands are an Australian Territory in the eastern Indian Ocean, and comprise an atoll that has had a particularly significant place in the development of coral reef studies. This was the only coral atoll that Charles Darwin visited during the voyage of the *Beagle*, and it therefore played a particularly central role in his theory of reef development. It was subsequently visited by several other naturalists. The horseshoe-shaped atoll has a series of sandy reef islands around its rim and a central lagoon that is relatively well flushed during southeast tradewinds, but incompletely flushed during times when winds blow from the northwest.

### History

The Cocos (Keeling) Islands were probably first sighted by Captain William Keeling in 1609. Captain James Clunies Ross visited the islands in 1825 and cleared some vegetation for a settlement. Clunies Ross worked for Alexander Hare who settled on the islands in 1826 with a small entourage of workers, and Clunies Ross himself returned in 1827 and commenced an alternative settlement. Relations between Clunies Ross and Hare deteriorated until Hare left the islands in 1831, after which Clunies Ross' family, known as "Kings of the Cocos," ran the islands as a coconut plantation. In 1955, they became a territory of Australia, and in 1978 the Australian government purchased all the land, except Oceania House, Clunies Ross' residence, and the surrounding grounds.

The atoll became particularly associated with coral reefs because it was visited from 1 to 12 April 1836 by Charles Darwin aboard *HMS Beagle*. During the voyage across the Pacific, Darwin had deduced his remarkable "subsidence" theory of coral reef development in which he considered that a mid-ocean volcanic island would first be encircled by a fringing reef, but that through gradual subsidence of the volcanic basement and vertical growth of the surrounding reef, this would progress through a barrier reef stage, ultimately becoming an atoll. Darwin made a number of insightful observations on the Cocos (Keeling) Islands, but he was particularly pleased because he felt that shoreline erosion and undercutting of coconut trees on West Island supported his theory that the atoll was slowly subsiding. Cocos featured prominently in Darwin's book on coral reefs (Darwin, 1842).

The Cocos (Keeling) Islands were subsequently visited by several other naturalists, in some cases advocating support for alternative theories (Woodroffe and Berry, 1994). Particularly, detailed observations of the reef islands and an estimate of the sediment budget were made by Henry Brougham Guppy during 1888 (Guppy, 1889). Guppy's visit was funded by John Murray and several of his observations consequently supported an alternative view advocated by Murray that atolls built out horizontally through progradation of the reef front. A descriptive account of the islands appeared in a book entitled *Coral and atolls* by Wood-Jones, who spent a year there as the medical doctor during 1905–1906 (Wood-Jones, 1912). Extensive collections of the fauna and an analysis of the historical significance of Clunies Ross' writings were undertaken by Gibson-Hill (1953) and an account of Darwin's time on the atoll was compiled by Armstrong (1991).

### Atoll morphology and physical characteristics

The Cocos (Keeling) Islands comprise a southern horseshoe-shaped atoll (South Keeling Islands, hereafter referred to as Cocos) with more than 20 sandy reef islands around a shallow lagoon (Figure 1), and a northern reef island with a small remnant lagoonlet, North Keeling. These rise from an ocean floor that is about 5,000-m deep, and are the only seamounts within the discontinuous Vening Meinesz chain to reach sea level, making Cocos one of the more isolated atolls.

Cocos is dominated by the southeast trade winds and has persistent swell from the southeast for most of the year, refracting around the atoll but breaking on the entire perimeter. Tidal range is 1.1 m at springs, and the atoll is influenced by occasional tropical cyclones, although there is little evidence of severe storms on the reef flat which does not have large reef blocks or shingle ridges typical of more storm-prone atolls in the Pacific. During short periods, particularly in El Niño years when there are only light winds from the northwest, lagoonal flushing is reduced and episodes of fish kill and coral death have been recorded.



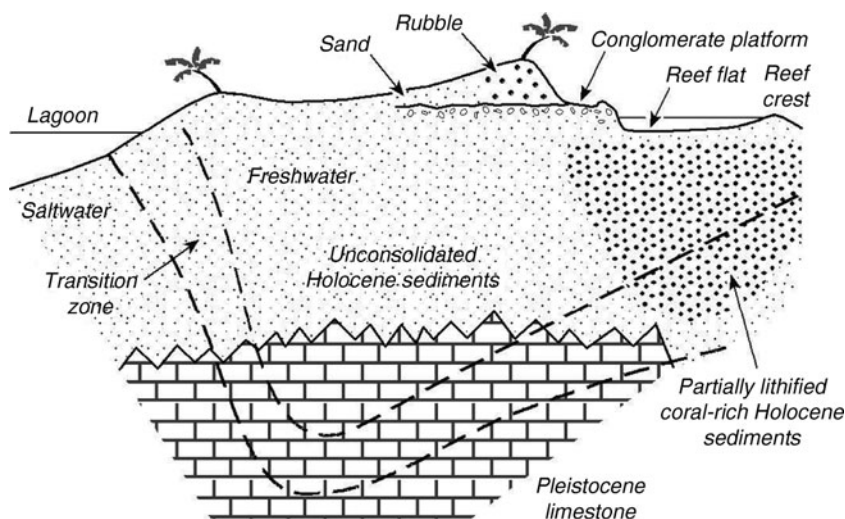
**Cocos (Keeling) Islands, Figure 1** A SPOT satellite image of the main atoll of the Cocos (Keeling) Islands, showing the horseshoe-shaped rim on which the reef islands occur. The lagoon is 8–14-m deep in the north, but contains a reticulate pattern of reefs and numerous blueholes in its southern part, with incursion of sand carried across the reef flat and deposited as sand aprons at the lagoonward terminus of interisland passages. The dark, purplish blue areas in the lee of the two elongate islands (West Island and South Island) are seagrass-covered sand flats (Image sourced from the Cocos (Keeling) Islands Geographical Information System, Geoscience Australia).

### Atoll rim and Lagoon

The horseshoe-shaped rim of the atoll is near continuous except in the northern part where there are openings 12–14-m deep, on the western and eastern side of Horsburgh Island. Drilling and radiocarbon dating indicate that the Holocene rim has accumulated over the Last Interglacial reef limestone encountered at depths of 10–14 m below sea level (Woodroffe et al., 1994) (Figure 2). This older limestone, which represents the rim of an atoll that formed the last time the sea was at or close to its present level, is extremely porous and it plays a significant role in the groundwater hydrology of the atoll (Woodroffe and Falkland, 1997).

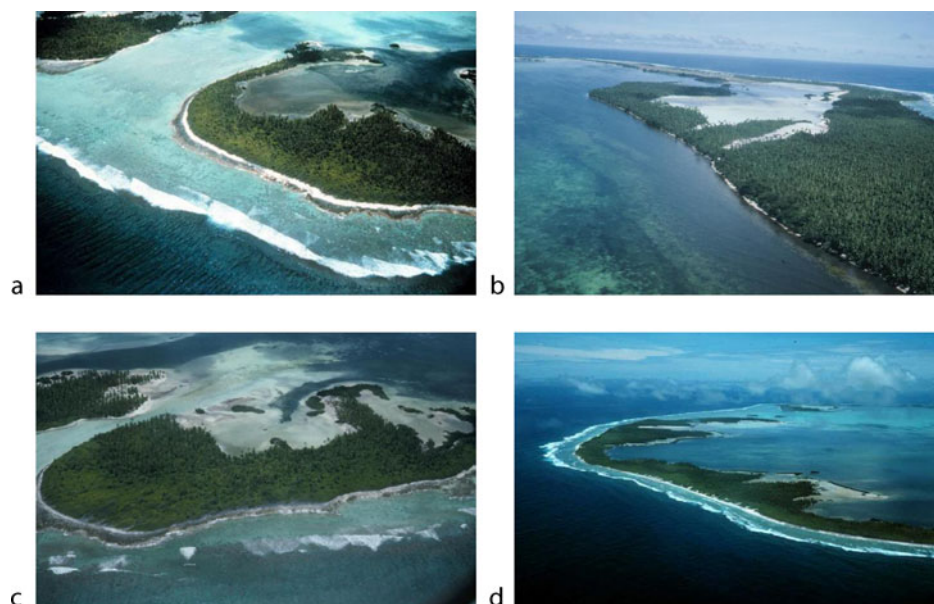
The lagoon covers about 190 km<sup>2</sup> and comprises a number of distinct areas. There are shallow sand flats that occur in the lee of South Island, which dry at lowest tides, and support a cover of seagrass. Much of the southern part of the lagoon comprises a reticulate pattern of reefs, some of which are 0–3-m deep, others which are exposed at the lowest tide. This network of reefs separates deeper holes, termed blueholes. These reach 20 m or more deep and have a sporadic cover of branching or foliose corals, much of which is dead. They harbor sharks in their murky waters. The northern lagoon is 8–12-m deep and floored largely with sandy sediments.

The lagoon is incompletely flushed because the inter-island passages are shallow and many dry at low tide (Figure 3a), limiting their effectiveness for the exchange of water from the ocean (Kench, 1998; Kench and McLean, 2004). Sediment is carried into the lagoon and there are sand sheets that are gradually infilling the southernmost blueholes (Smithers et al., 1993). Minor lagoonlets, termed teloks (Figure 3b), occur on the lagoon side of the larger elongate islands. These are very shallow and muddy areas separated from the ocean by a ridge.



**Cocos (Keeling) Islands, Figure 2** Schematic cross-section of the atoll (based on drilling results in Woodroffe et al., 1994). The depth at which the underlying Pleistocene limestone is encountered varies from 8 to 14 m, and reef islands are up to 800-m wide.





**Cocos (Keeling) Islands, Figure 3** Aerial oblique views of the rim of Cocos: (a) Pulu Pandan and the passage to the south of it, on the eastern rim of the atoll; (b) West Island showing the telok (lagoonlet); (c) one of the smaller islands on the eastern rim of the atoll; (d) South Island (Photos C. Woodroffe).

There are minor ridges developed on the lagoon shore, and the teloks experience restricted exchange of water with the lagoon. A similar sequence of ridges, resembling a crab claw, extend on either side of the southern passage, and the distinct succession of ridges that extend from the southeastern shore of West Island appears to be gradually decreasing water movement over the intertidal flats in their lee.

There are extensive areas of the atoll rim and of the lagoon flats that are intertidal and which shoal, or dry, at the lowest tides (Figure 3c). These have provided an environment in which large colonies of *Porites*, including both a massive species and a branching species, have grown upward to a point at which their upward growth is constrained by exposure during the lowest tides. This microatoll growth form was first described from Cocos by Guppy, and has become a focus for research, because the upper surface provides a low-resolution record of past water level. Extensive survey of these corals around the margin of Cocos has shown the subtle variations that exist in the elevation at which this upper limit to coral growth occurs (Smithers and Woodroffe, 2000). The upper surface morphology across two of the larger specimens has enabled an insight into water-level changes relative to this atoll over the past century, indicating minor oscillations in the limit of coral growth and a slight rise in water level that is generally less than that inferred from tide gauges from around the world (Smithers and Woodroffe, 2001).

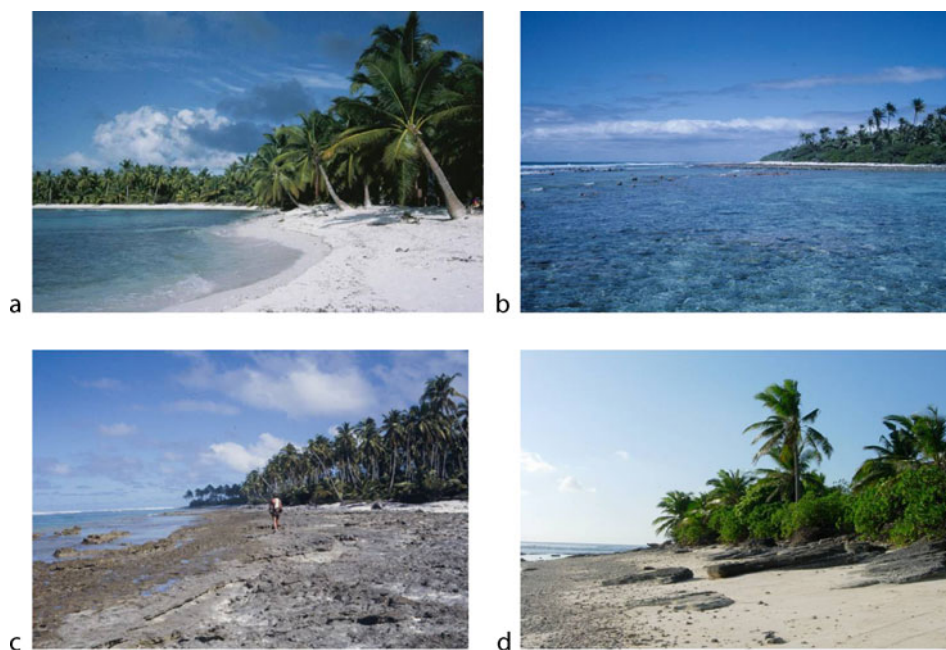
### Reef islands

Figure 1 shows a SPOT satellite image of the horseshoe-shaped atoll and the islands on its rim (Figures 4a and 4b).

There are two major elongate islands, West Island and South Island which occupy about 60% of the southern rim of the main atoll (Figure 3d). The remainder are small crescent-shaped islands, separated by inter-island passages, most of which shoal at low tide. Horsburgh Island on a lone reef at the north of the atoll, is shaped by wave refraction and reaches elevations of 3–4 m. The majority of islands are perched on a conglomerate platform. Guppy (1889) suggested that this represented a former reef flat, a view supported by Woodroffe et al. (1990). Conglomerate platform (termed brecciated coral-rock by Darwin (Figure 4c), reef conglomerate by Guppy and breccia platform by Wood-Jones) generally reaches up to 0.5 m above MSL, although locally reaching 1 m, and is inundated by waves at the highest tides.

Radiocarbon dating of fossil corals from within the conglomerate indicates that it was formed 4,000–3,000 years BP (Woodroffe et al., 1994). Locally, several corals in their growth position have been identified growing at an elevation above that to which they are presently able to grow. Several of these corals are massive *Porites* that adopted a microatoll form, whereas others are branching *Porites*. These corals provide evidence that the former reef flat was formed around 3,000 years ago when the sea was 50–80 cm higher than it is now with respect to Cocos (Woodroffe et al., 1990).

Darwin drew a schematic cross-section of “Keeling atoll” (although Darwin’s notes indicate that the cross-section was not actually of Cocos, but of Whitsunday Atoll) showing the prominent algal rim (at the reef crest), a near horizontal reef flat, the conglomerate platform (which he termed ledge of coral rock) (Figure 4c), and



**Cocos (Keeling) Islands, Figure 4** Characteristic shorelines of Cocos: (a) Trannies beach at the northern end of West island; (b) a broad reef flat on the eastern rim; (c) extensive conglomerate on the southwestern end of Horsburgh Island; (d) beachrock at the southern end of West Island (Photos C. Woodroffe).

the seaward ridge of the island, steeper on the oceanward side and sloping gradually toward the lagoon. Figure 2 shows a typical section of the eastern rim of the atoll. Many of the islands show the typical cross-sectional morphology that was sketched by Darwin, comprising an oceanward ridge crest, a lower-lying central area, and a less prominent lagoonward ridge. Islands are predominantly sandy, although with shingle in some places, and coral boulders along the oceanward shore of those on the eastern rim where the reef flat is narrowest. There are a number of outcrops of beachrock, bedded dipping parallel to the modern beach, along several of the oceanward beaches (Figure 4d), and occasional outcrops of cay sandstone, which is horizontally bedded and less well lithified.

Darwin inferred different formative processes for islands on windward and leeward sides of the atoll. On the windward (eastern) side he considered that islands accreted solely by addition of material on the oceanward shores, whereas on the leeward (western) side he envisaged that island growth resulted from a combination of oceanward accretion, augmented by lagoonward addition of sediment by waves from the lagoon. By this mechanism, Darwin accounted for the wider islands on the leeward of the atoll. Radiocarbon dating has provided some support for this pattern of accretion on West Island which seems to have accumulated primarily by oceanward accretion, but also with some lagoonward growth (Woodroffe et al., 1999). The crescent-shaped islands on the eastern margin of Cocos were described in detail by Guppy (1889) who proposed a model for their growth involving

spit elongation driven by unidirectional currents through the inter-island channels. This evolutionary model has not been fully tested by dating.

Islands are highest along their oceanward side. The oceanward beach ridge is generally 3–4 m above MSL; however, in some places the fine sand is winnowed from the beach by wind and the beach ridge is topped by a dune. Such dunes are not typical of atoll reef islands in general. South Island has a dune ridge 6–7-m high, reaching as high as 11 m on the southwestern corner of South Island. West Island, which remains the administrative center, has an oceanward ridge that is characteristically 3–4 m above MSL (much of the southern part of this island has been altered during runway construction), but rises to 7 m above sea level in the area where residential buildings have been constructed on a dune. On Home island, where the Cocos Malay kampong is found, the oceanward ridge generally reaches an elevation of 3 m above MSL, but at one location a dune rises up to 5 m (Woodroffe and McLean, 1994).

## Summary

The Cocos (Keeling) Islands consist of the main atoll of Cocos, and the isolated North Keeling (Pulu Keeling) which is Australia's smallest Commonwealth National Park. These rise from deep water, and the southern atoll consists of a near continuous rim with linear islands on the southern margin and a series of crescentic islands on the eastern side. The islands are anchored in their present

location by an underlying conglomerate platform that was formed as a reef flat in mid Holocene when the sea level was higher than present. The islands themselves are largely sand, with restricted dune development on the most exposed oceanward shore. Their elevation is generally 3–4 m above modern sea level, and as the latest tide gauge, installed in 1992, shows evidence of sea-level rise, signs of inundation in the lowest-lying areas may be an omen of more frequent flooding in future (Woodroffe, 2008).

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## Cross-references

Atolls  
 Blue Hole  
 Conglomerates  
 Darwin, Charles (1809–1882)  
 Eastern Indian Ocean – Northern Sector  
 Indian Ocean Reefs  
 Microatoll  
 Subsidence Hypothesis of Reef Development

## COLD-WATER CORAL REEFS

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## Synonyms

Deep-water coral reefs

## Definition

*Cold-water coral reef*. Qualitative term depicting the general contrast to warm-water coral reefs in the tropics and subtropics. The ambient seawater temperature range of known cold-water reefs is 4–14°C. The primary framework is constructed by colonial, azooxanthellate Scleractinia.

*Deep-water coral reef*. Qualitative term describing the general bathymetric setting of these reef systems, which is deeper than 40 m water depth but with the majority thriving in 200–1500 m depth.

## Introduction

Since Linnean times in the eighteenth century, it is known that azooxanthellate corals form substantial aggregations in cold and deep waters and in geographic regions far beyond the shallow-water coral reef belt of the lower latitudes. Until the 1970s, research and sampling of corals in deep waters was restricted to single beam echo soundings and dredge hauls. First visual documentations of this type of ecosystem came from drop cameras and few manned submersible operations, which shed more light in some cold-water reef environments (Squires, 1963; Wilson, 1979). The development of advanced hydro-acoustic sounding systems, such as swath bathymetry and the wider assessment of remotely operated vehicles (ROVs), initiated a worldwide burst to study cold-water coral ecosystems all over the world supported by multinational strategic research programs, which attracted biologists, geologists, and oceanographers to better understand the environmental controls and functionality of this cosmopolitan type of coral ecosystem. Of the 711 known azooxanthellate scleractinian species, 622 live in water depths deeper than 50 m, but only a small group of 6 species is capable to construct reefal framework with *Lophelia pertusa* and *Madrepora oculata* as the most



important cosmopolitan representatives (Messing et al., 2008; Roberts et al., 2009a).

### Dimensions and time constraints of cold-water coral reefs

Cold-water coral reefs are self-sustained and spatially well-defined coral framework-sediment systems measuring tens of meters to kilometers in lateral extension and up to 40 m in thickness, thus influencing local current regimes (Dorschel et al., 2007; Mienis et al., 2007). Most cold-water coral reefs occur in water depths of 200–1500 m, where light is almost reduced or absent, although some reefs exist in much shallower depths due to specific hydrographic conditions, that is, in some upwelling fjord settings (Freiwald et al., 2004; Försterra et al., 2005; Roberts et al., 2006). Reefs generally occur in groups of hundreds if not thousands in a given area like on many places of the Norwegian continental shelf, or off Apulia, Ionian Sea (Fosså et al., 2005; Savini and Corselli, 2010). A focus on the Norwegian coral systems may underpin the substantial reef-constructing capability of these unexpectedly large coral build-up seabed structures. The last glacial ice shields vanished from the shelf about 13–12 ka ago, and the first appearance of *Lophelia* corals was dated 11 ka, short after the last major cold spell, the Younger Dryas Event, from one of the northernmost coral reef provinces in northern Norway (Lopez Correa, unpublished data). This coral age and the high latitudinal position coincides with the onset of the modern oceanographic regime in the north eastern Atlantic, the full establishment of the poleward flowing Atlantic Current system, which seemingly had carried coral larvae as North as to the Stjernsund, Finnmark District. This allows the following assumption. All the cold-water reefs in Norwegian shelf and fjord settings formed within the past 11 ka. This is a relatively short time span to develop mature biogenic seabed structures with the dimensions given above. Performing a first conservative calculation of the  $\text{CaCO}_3$  flux and production rates for cold-water corals, Lindberg and Mienert (2005) concluded that Norwegian corals contribute with flux and production rates reaching 4–12% of that of warm-water reefs. Further south, post-glacial onset of cold-water coral growth in the Porcupine Seabight and southeast Rockall Bank recolonized fossil cold-water carbonate mounds at and after 11 ka, contemporaneously with the onset of the Norwegian coral spread towards the North (Frank et al., 2009). Even further south, cold-water corals fade off just after the Younger Dryas period in the Gulf of Cádiz (Wienberg et al., 2009). The least we can conclude from these data of rise and decline ages is that reef-constructing *Lophelia* and *Madrepora* quickly responds to changing climates and productivity regimes along the northeastern Atlantic continental margin.

### Colony, thicket, coppice, reef

Another apparent character is the low diversity of the primary coral framework constructing species. In contrast to warm-water coral reef framework, only one to three

colonial scleractinian species form the backbone of cold-water reefal framework in a given area (Stanley and Cairns, 1988), thus acting as typical ecosystem engineers. Most significant framework-forming azooxanthellate scleractinians are *L. pertusa*, *M. oculata*, *Solenosmilia variabilis*, *Goniocorella dumosa*, *Enallopsammia profunda*, and *Oculina varicosa*. The latter species lives with endosymbiotic zooxanthellae in the photic zone but without photo-endosymbionts in aphotic depths (Reed, 2002).

The initiation of what will become a reef eventually with time starts with a dense larval spatfall of one or two of the above-mentioned species within a relatively localized area. After metamorphosis of the settled larvae, the corals develop colonies that steadily intermingle with neighboring colonies with time, thus increasingly monopolizing the seabed to form low-relief *thickets* of 10–30 cm height (Squires, 1964). Such thickets provide support and shelter for other organisms that become attracted to the newly created habitat. The corals protect themselves efficiently against competitors with their anti-fouling ability – the skeleton-overcoating tissue or coenosarc. The tissue spread upon those organisms that try to settle onto the coral skeleton, which subsequently becomes encalcified by tissue-controlled precipitation of faint aragonite layers to entomb the epizoids (Harmelin, 1990; Freiwald and Wilson, 1998). With continuing growth of coral colonies within a thicket, a separation of live from dead and tissue-barren framework induces a further important step in the evolution of a complex ecosystem, which is called the *coppice* stage. The tissue-barren framework is now prone to colonization by other sessile organisms, such as foraminifers, hydrozoans, octocorals, serpulids, molluscs, bryozoans, brachiopods, and a diverse array of sponges among others. Therefore, species richness of the coral-associated assemblage of sessile organisms is more diverse in the tissue-barren part of a coral colony than in the upper live part of the colony resulting in a clear faunal zonation pattern (Freiwald, 2002; Mortensen and Fosså, 2006). Of some importance is the infestation of the tissue-barren coral framework by boring and endolithic organisms, which opens a new dimension in micro-habitat colonization but also tend to weaken the framework stability through bioerosion. Most effective bioeroders are boring alecionid, clionaid, and phloeodictyid sponges, which deeply excavate the coral skeleton, thus facilitating the collapse of a colony or even larger parts of thickets (e.g., Beuck and Freiwald, 2005; Beuck et al., 2007, 2010). In the coppice stage, accumulation of coral fragments and remains of the associated skeletal fauna becomes prominent. However, another pre-requisition is needed to transform coppices into a high-relief reef stage – continuous trapping and baffling of suspended particles advected by the bottom-near current regimes. These imported particles entirely consist of the remains of pelagic organisms, such as planktonic foraminifers, coccolithophorids, and pteropods, or they represent a mixture of pelagic and terrigenous silt and clay particles, which are then called hemipelagic sediments. In any case, the matrix infill

between the dead coral framework, either pelagic or hemipelagic, largely contributes to the relief-forming growth of a given reef structure. Without this additive, pure coral framework would disintegrate by processes like bioerosion (see above) and would end as a low-relief coral rubble substrate. Sediment trapping is facilitated by the current velocity decelerating effect of the coral framework, by the mucus binding of particles, and is probably enhanced by large quantities of arborescent agglutinated benthic foraminifers, which live attached to coral skeletons, thus enhancing the baffling capacities considerably (Messing et al., 2008). Particle flux in cold-water coral settings shows a pronounced seasonality as a matter of pelagic production cycles in the fertile surface waters (Duineveld et al., 2007). In general, the current regime at depths of the corals keeps sedimentary particles in suspension and therefore, off-reef sedimentation rates are low if any. The intermingling of biological with geological processes, such as new colonization, coral growth, with subsequent trapping and deposition of suspended fine-grained particles within the loci of coral reefs, is regarded as the main driver to enhance the formation of elevated reef structures within fairly short time scales (Roberts et al., 2006, 2009a and see above).

### Coral habitats, some key species and trophic webs

Mature reefs provide a variety of macro- and microscale habitats, which enhance biodiversity compared to adjacent off-reef habitats. According to Mortensen and Fosså (2006), macro-habitats in a typical reef consist of the *live coral zone* on top and upper flanks, then the *dead coral zone*, which consists of older in situ or fragmented coral framework underneath, and at the base, a belt of *coral rubble zone* mixed with background sediments that surround the structure. Micro-habitats are the surfaces of tissue covered living corals, the detritus laden surface of dead corals, the cavities inside dead coral skeleton, and the free space between coral branches. The live coral zone shows only few characteristic species that cope with the protective and reactive coenosarc of the corals. The eunicid polychaete *Eunice norvegica* is regarded as a non-obligate mutualist that takes food from the corals, cleans the polyps from sediment particles, and stimulates precipitation of coral skeleton to build a protective tube inhabited by the worm (Mortensen, 2001). Moreover, *E. norvegica* is able to actively aggregate pieces of small coral colonies, thus enhancing coral patch formation (Roberts, 2005). Another polychaete frequently observed on living corals is the polynoid *Harmothoe oculinarum* (Jensen and Frederiksen, 1992). The rosalinid foraminifer *Hyrrokin sarcophaga* is known as a common parasite of cold-water corals and associated fauna, such as the file clam *Acesta excavata* (Cedhagen, 1994; Freiwald and Schönfeld, 1996; Beuck et al., 2008). Predatory gastropods in the living coral zone, probably grazing coral tissue and mucus are several coralliophilinid species such as *Babelomurex sentix* and *Coralliophila richardi* (Taviani et al., 2009).

Other characteristic grazers commonly observed in the living coral zone are starfishes like *Porania pulvillus* (Wienberg et al., 2008). Sponges strongly associated with live corals are *Hexadella detritifera*, *Lissodendoryx diversichela*, *Hymenaphia verticillata*, and *Mycale lingua* (e.g., van Soest et al., 2005, 2007). None of the species mentioned above is obligate to cold-water corals, but seemingly they occur in greater abundances in this habitat. The dead coral zone shows highest diversity of coral associates (Mortensen and Fosså, 2006), which use the complex coral framework in various ways but mostly as hard substrate. Only focusing on bivalves here, some characteristic species are *A. excavata*, *Asperarca nodulosa*, *Bathyarca pectunculoides*, *Chlamys sulcata*, and *Delectopecten vitreus*, among many others. Moreover, the coral skeleton is utilized by a vast array of boring organisms; the ones which have an endolithic lifestyle among them are fungi, sponges, polychaetes, and bryozoans (see Beuck and Freiwald, 2005; Beuck et al., 2007, 2010; Wisshak et al., 2005).

Along with increasing research efforts on cold-water coral reef systems, it became increasingly clear that especially the framework-building *L. pertusa* acts as an ecological engineer by providing a variety of habitats, shelter, substrates, and by provision of particulate and dissolved organic matter, thereby attracting a myriad of species (Roberts et al., 2009a; Wild et al., 2008). Regional species filing useful for estimations of gamma diversity found with *Lophelia* started with 895 species (see the seminal review of Rogers, 1999), and later on with 1,300 coral-associates. A current database for the HERMIONE Project of the European Commission listed nearly 2,900 species sorted out for synonyms and calibrated taxonomy using the World Register of Marine Species database ([www.marinespecies.org](http://www.marinespecies.org); Freiwald, in preparation) of which 140 species were described new to science from this reef system during the past 15 years. The most diverse taxa are crustaceans (493 species), mollusks (420 species), sponges (386 species), cnidarians (338 species), and fishes including sharks and rays (278 species). It should be noted that many taxa are yet not sufficiently treated and validated by experts, and that even in well-studied coral sites sampling efforts are yet under-representative to provide a solid base for quantitative biodiversity studies to better understand the entire community and their ecological functioning. Most advanced biodiversity studies from cold-water reefs were provided by Jonsson et al. (2004) from the Swedish Kosterfjord, from Mortensen and Fosså (2006) comparing several reefs from within and off the Norwegian Trondheimsfjord, and from Roberts et al. (2009b) with a study on the Scottish Mingulay reef system.

Unlike warm-water reefs, which also rely on solar radiation as intimate energy resource, cold-water coral reefs are largely dependent on the export of organic matter from primary production in photic surface waters to the seafloor (Duineveld et al., 2007; Davies et al., 2009). In a first comprehensive study of the trophic food web and food supply

from coral habitats along the southeastern Rockall Bank slope, Duineveld et al. (2007) noted a remarkable paucity of deposit-feeders compared to abyssal communities and a short trophic length of the food chain dominated by filter-feeders, added by predators and scavengers. The major food source is from suspended particles. However, our present knowledge is limited if not contradictory as to what extent zooplankton forms a significant part of the suspended load (see Duineveld et al., 2007 for discussion).

## Summary

In the recent years, knowledge on the general distribution, biology, geology, and hydrography has generated a wealth of information on the subject of cold-water coral reefs and their associated communities through the application of state-of-the-art marine instrumentation (Roberts et al., 2009a). Cold-water coral reefs are formed by a small group of colonial azooxanthellate scleractinians as biological engineers and thereby providing a great variety of habitats attractive for a diverse associated community. These framework-constructing corals trap suspended sedimentary particles to generate a three-dimensional structure within an astonishingly short time and at rates comparable to some tropical shallow-water coral reef systems.

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## Cross-references

Aragonite  
 Bioerosion  
 Carbonate Budgets and Reef Framework Accumulation  
 Corals: Biology, Skeletal Deposition, and Reef-Building  
 Holocene Reefs: Thickness and Characteristics  
 Molluscs  
 Nutrient Pollution/Eutrophication  
 Sediment Dynamics  
 Sponges  
 Swathe Mapping  
 Taphonomy

## CONGLOMERATES

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## Synonyms

Conglomerate pavements; Conglomerate platforms; Conglomerate promenades; Exposed limestone coral; Rampart-rocks; Shingle conglomerate

## Definition

Conglomerates are defined as exposed, cemented reef-derived detritus, dominantly composed of coral rubble.

*Environment:* mostly, windward sides of reefs; occasionally, on leeward sides near passes and channels.

*Morphology and structure:* Conglomerates exhibit either a planar, mainly horizontal surface (“platform”) or steeply dipping ( $>20^\circ$ ) beds to lee (“basett edge”). Each platform usually has a fairly constant elevation relative to the present mean sea level. But the heights can vary between 0.6 and 1.0 m in areas subject to microtidal regimes and about 1.0–3.5 m in areas subject to macrotidal conditions. Their internal structure reveals the superimposition of distinct beds varying in thickness and grain size, thus reflecting changes in sediment supply and water energy. Locally, there are large coral boulders embedded in the rubble.

*Lithology and diagenesis:* The conglomerate matrices are poorly sorted grainstones, packstones and rudstones. Diagenetic features include typical marine cements (e.g., irregular or isopachous rims of fibrous aragonite, high-magnesian calcite, peloidal micrite) locally showing geotrophic (pendant) habits.

*Origin:* Conglomerates are interpreted as generated by storms and cyclones. These are probably the counterparts of shingle and gravel sheets and ramparts today, accumulated close to sea level. Accordingly, the horizontal surface is generally believed to be primary in origin.

*Age of deposition:* radiocarbon dating of coral and molluscan fragments suggests that deposition occurred between less than 1,000 and about 6,000 years BP in the Pacific.

*Potential use:* indicators of mid-late Holocene sea-level changes.

## Parental features

[Bassett edges](#), [boulder ramparts](#), [cemented platforms](#), [shingle ridges](#), [beach-rocks](#).

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## Cross-references

[Antecedent Platforms](#)  
[Atoll Islands \(Motu\)](#)  
[Bassett Edges](#)  
[Beach Rock](#)  
[Boulder Zone/Ramparts](#)  
[Megablocks](#)  
[Platforms \(Cemented\)](#)  
[Shingle Ridges](#)

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## CONSERVATION AND MARINE PROTECTION AREAS

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## Definitions

Conservation is an ethic of resource use, allocation, and protection, with a primary focus upon maintaining the health and biological diversity of the natural world.

Cumulative impacts are the change in the environment which results from the incremental impact of two or more individual events which, when added to other closely related past, present, and reasonably foreseeable probable future events, will compound, magnify, or increase each other or their own environmental impacts.

Ecosystem-based management is an integrated approach to management that considers the entire ecosystem, integrating the ecological, social, economic, and institutional perspectives, and emphasizing the protection of ecosystem structure, functioning, and key processes.

Marine management is a continuous, interactive, adaptive, and participatory management process, comprising a set of related tasks, which collectively work towards achieving a desired set of goals and objectives.

Marine protected area (MPA) network is an organized and systematic collection of individual MPAs, connected in some way by ecological or other processes.

Protected area is a clearly defined geographical space, recognized, dedicated, and managed through legal or other effective means to achieve the long-term conservation of nature with associated ecosystem services and cultural values (Dudley, 2008). Hence, an MPA is a protected area within the marine (intertidal or sub-tidal) realm.

## Introduction

In many parts of the world, coral reefs have been actively conserved for centuries to ensure continuing access to food sources such as fish and shellfish. In most western countries, however, the need to protect coral reefs, and the importance of conserving marine areas, has only been recognized in the last 50–70 years.

Problems arise when marine and coastal resources, such as coral reefs or their resident species, are considered as “open to everyone” with “free” access to virtually all users. Often referred to as “The Tragedy of the Commons” (Hardin, 1968), this commonly leads to excessive use and habitat degradation. These generalizations, of course, vary between countries according to cultural perceptions of private, public, and common property.

The long-held belief that marine resources were almost unlimited and inexhaustible has now proven to be a myth; many living marine resources may be renewable if harvested sustainably, but there are finite limits to marine exploitation. Today, as never before, there are many more pressures on marine environments and a growing awareness of the *cumulative impacts* of those pressures. There are many striking examples around the world of the consequences of poorly managed coral reefs or untimely responses to warning signs.

*Marine protected areas* (often abridged to the term MPAs) are one of a variety of practices at the international, regional, national, and local level to protect coral reefs. Other conservation strategies are being applied at a range of scales from international agreements to local community-based management areas.

Globally, the rate of coral reef degradation, however, greatly exceeds the rate of effective coral reef conservation; hence, far more needs to be done to effectively protect coral reef systems – arguably the most biologically diverse ecosystems on the planet.

## Status of coral reefs globally

Pressures on coral reef systems can be regarded as either human-induced (e.g., mining/quarrying, unsustainable fishing, pollution, heavy-metal impacts, climate change, technological innovations enabling greater use) or natural events (e.g., cyclones, tsunamis). The effects of such pressures on coral reefs can range from negligible to catastrophic, and can be episodic or chronic. It is also important to recognize issues such as *cumulative impacts* (both direct and indirect) and the synergistic effects of such pressures, none of which is easily considered. The combined chronic effects of over-fishing, by-catch, habitat

degradation, pollution, and food-web changes have had significant impacts, resulting in formerly abundant species now being rare and marked changes in resource utilization.

The 2008 Status Report of the World's Coral Reefs (Wilkinson, 2008) estimates that 19% of the world's original reefs are effectively lost forever; 15% are seriously threatened with loss likely in next 10–20 years; and 20% are under threat of loss in 20–40 years. The latter two estimates are made without considering the looming threats of global climate change or that effective future marine management may conserve more coral reefs. If current pressures continue, some consider that 60% of the world's coral reefs may be severely damaged by 2050.

### Key threats to marine conservation and especially coral reefs

1. *Climate change* – Climate change impacts on coral reefs and marine ecosystems are already having marked environmental effects, and the consequent impacts are likely to flow onto the industries that depend on these areas as well as coastal communities. The impacts of climate change on marine biodiversity are being observed throughout the world – carbon dioxide concentrations have increased dramatically in recent decades; the oceans are warming and becoming more acidic, frequently bleaching large areas of coral; and sea-level rise is now flooding some coastal communities.

2. *Land-based water quality* – Coral reefs can be impacted by a variety of land-based pressures including agricultural runoff, inadequate sewage and stormwater treatment, siltation from coastal development, deforestation or beach re-nourishment projects, contamination from petroleum products, etc.

Agricultural runoff can contain herbicides, pesticides, and nutrient fertilizers. Elevated levels of nitrogen and phosphorus may result in algal blooms that can potentially grow much faster and out – compete corals.

Human sewage, often untreated, can add nutrients, microorganisms, and other pollutants to coral reefs and can cause eutrophication.

3. *Unsustainable harvesting (fishing or collecting)* – Unsustainable harvesting can cause a variety of negative impacts on coral reefs, including altering trophic interactions causing indirect environmental effects. For example, where predators have largely been removed, increases in the population of their prey have resulted in unexpected flow-on effects. Unsustainable fishing or the depletion of fish spawning sites can also reduce genetic variation in a population, making it harder for species to adapt to environmental change.

Over-fishing can have major impacts on target species and has led to the extinction of species in some areas (e.g., Queen Conch), but can also have major impacts on non-target species (by-catch) as well as cause habitat destruction.

Discarded fishing gear (e.g., ghost nets) can damage reefs and also have major impacts on marine biodiversity. Marine debris, especially plastics and monofilament fishing line, can abrade corals and prove lethal for birds, fish, and turtles that become entangled in it or mistake it for food and ingest it.

4. *Direct physical damage (e.g., blast fishing, dredging, mining, infilling, etc.)* – Many fishing practices harm coral reefs by physically damaging habitat or by killing non-targeted species. Blast fishing occurs in some parts of the world, whereby underwater explosions are used to injure fish so that they float to the surface where they are easily captured. The blast, however, also destroys coral and flattens the reef structure. In some places, fishermen use cyanide or other poisons to stun fish so that they can be captured alive, but small fish and coral polyps may also be killed.

Limestone mining or infilling for coastal developments have obvious major impacts, completely destroying coral reefs or severely altering hydrological flow patterns.

The depletion caused by the harvest of coral and “live rock” for the aquarium/curio trade has damaged many reefs around the world.

5. *Indirect impacts from marine or coastal developments* – Human activities on land such as the building of ports, industrial infrastructure, deforestation, tourism facilities, or other coastal developments can lead to increased rates of sedimentation affecting adjacent reefs. High sediment loads can smother corals or decrease light penetration, thereby reducing the photosynthetic ability of the symbiotic algae in coral.
6. *Unsustainable tourism/recreation* – Anchors, accidental boat groundings, and propeller strike can all crush and scar coral. The fins of divers and snorkelers and even their diving equipment can inadvertently damage coral. Well-meaning tourists may feed reef fish, but this can change feeding behavior with other flow-on effects. Similarly, shell collecting, fossicking, and uncontrolled reef-walking can have detrimental impacts on corals.
7. *Invasive species (pest plants, animals, diseases) or outbreaks of native species* – Invasive marine species may be introduced by a variety of vectors, including ballast water discharge, biofouling on vessel hulls or within internal seawater pipes in commercial and recreational vessels, aquaculture operations (accidentally or intentionally) and aquarium imports, as well as marine debris carried by ocean currents.

At high densities, outbreaks of species that eat juvenile or adult corals can cause major problems for reefs and their associated species (e.g., the crown-of-thorn starfish, a long-spined species of sea urchin, and a small gastropod snail have all caused major problems in many coral reefs around the world).

The types and extent of diseases attacking corals have increased markedly in recent years and coral diseases such as Black Band and White Plague are



becoming more prevalent, especially following bleaching stress. Bacteria in sewage pollution are a suspected cause of White Band disease in corals.

8. *Shipping and related issues* – Oils and hydrocarbons inadvertently discharged, or deliberately washed overboard, can cause impacts, especially if they occur during coral spawning. Coral reefs and mangroves are more susceptible to the impacts of oil spills compared to sandy beaches or seagrass beds. Other ship-sourced threats include sewage discharge and toxic discharges, as well as the impacts of antifouling paint used on vessels.

### Effective reef conservation

An emerging realization is that effective marine conservation requires a lot more than just protecting areas in MPAs alone; in order to provide for the future, including any sustainable use, effective reef conservation requires the following:

1. Understanding, and effective management, of the wider context (i.e., the surrounding waters and the ecological processes that influence the coral reef as well as the nearby catchment areas); this means, in effect, integrated land/sea management;
2. Sustainable resource utilization (especially fishing and collecting) of the coral reef as well as the surrounding marine area;
3. Effective marine protection (which may be by declaring an MPA through a legal or other effective means);
4. Effective stakeholder involvement (industry and community); and
5. Where appropriate, the incorporation of traditional management approaches.

### Marine protected areas

In recent decades, considerable efforts have occurred worldwide to establish MPAs to improve marine conservation. A diverse array of MPA types, each with its own label and priorities, has arisen in coastal and marine areas throughout the world.

In this instance, MPA is used as a broad generic or “umbrella” term, reflecting the IUCN definition amended in 2008 of a protected area:

*A clearly defined geographical space, recognised, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values.*

IUCN has seven categories of protected area, ranging from highly protected “no-take” areas, intended only for scientific research (IUCN Category IA), through no-take areas that may be accessed by the public but where virtually all types of extraction are prohibited (IUCN Category II), to multiple-use areas in which the sustainable extraction or collection of natural resources may occur (IUCN Category VI).

One of the better known MPAs with coral reefs is the Great Barrier Reef Marine Park (GBRMP), covering

344,400 km<sup>2</sup> on Australia’s northeast coast. Because of the iconic status of the Great Barrier Reef, many people believe the entire area is a marine sanctuary or marine reserve, and therefore protected equally throughout. While the entire area is protected by law, many do not understand that the GBRMP is a multiple-use MPA, in which a wide range of activities and uses are allowed, including many extractive industries in certain zones (but not mining nor drilling for oil), while still protecting one of the world’s most diverse ecosystems (refer to the GBRMP Activity Matrix, [Figure 1](#)).

A major rezoning of the GBRMP occurred from 1999 to 2004, with the primary aim to improve the protection of the range of biodiversity throughout the GBRMP. The final outcome included an increase in “no-take” zones to over 33% of the entire area, with an additional 33% zoned to ensure comprehensive habitat protection (refer to map showing the zoning in the GBRMP, [Figure 2](#)).

The comprehensive, multiple-use zoning system in the GBRMP (which comprises IUCN categories IA, II, IV, and VI) is a systematic network that effectively governs all human activities, providing high levels of protection for specific areas, while allowing a variety of other uses, including shipping, dredging, aquaculture, tourism, boating, diving, commercial fishing, and recreational fishing, to occur in certain zones.

The most optimistic estimates indicate that less than 1% of the world’s oceans are currently in any type of MPA, and only a small proportion of coral reefs is adequately protected. While there are many effective MPAs, there are also many ‘paper parks’ that are not achieving what was intended when they were declared.

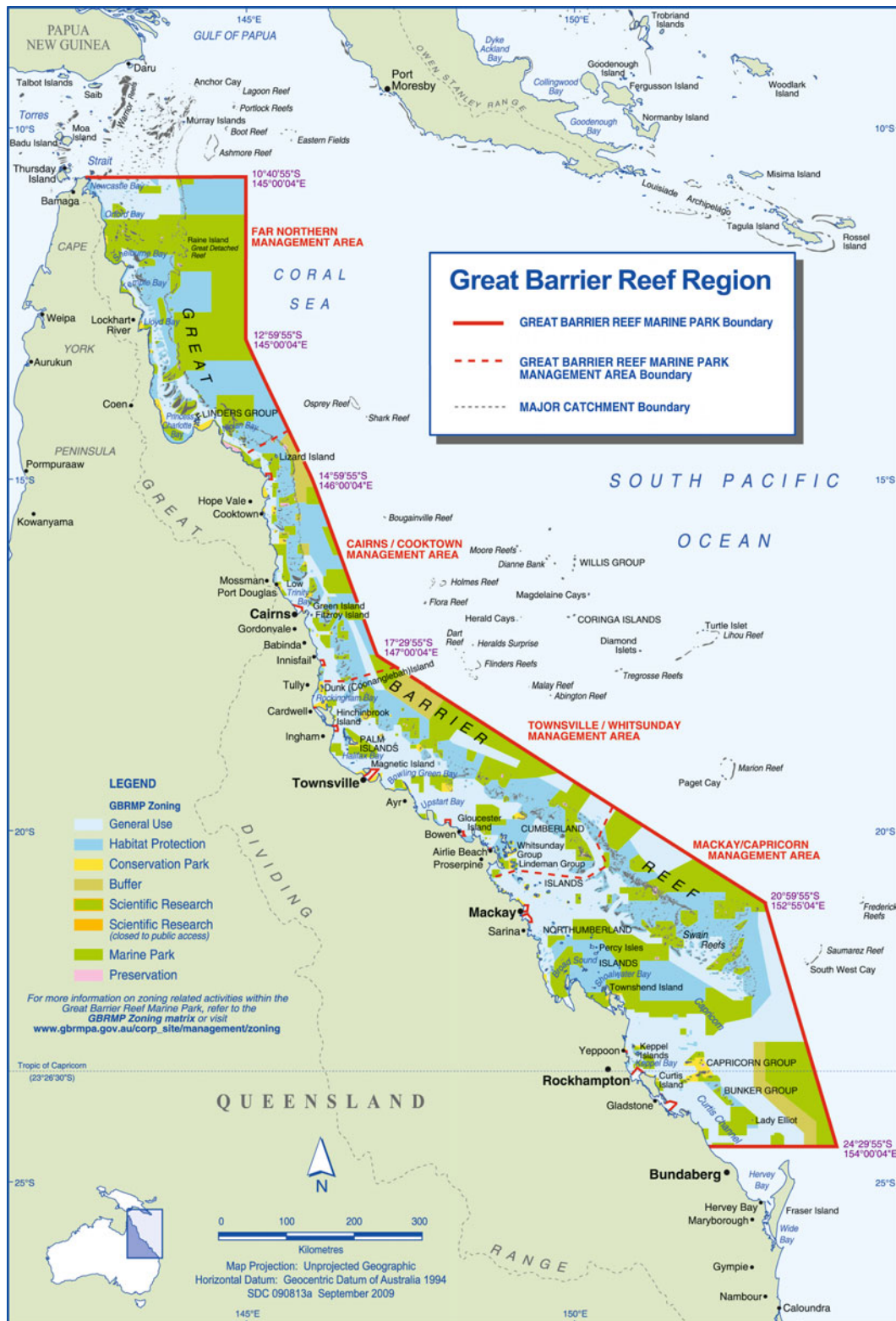
Recent declarations of several large MPAs, which include coral reefs such as Papahānomoukūakea (NW Hawaiian Islands) and the Phoenix Islands in the Republic of Kiribati, are encouraging, but collectively are still not enough to meet global targets set by international conventions such as the Convention on Biological Diversity.

### The benefits of MPAs

Single MPAs, particularly those containing appropriately chosen “no-take” areas, can provide a range of benefits including helping to maintain biodiversity, enhance nonconsumptive opportunities, and improve stocks that have commercial and recreational value in adjacent areas.

The benefits of MPAs, however, will be greatly increased if they are effectively linked to provide ecologically coherent networks. Any MPA network should be designed to link individual areas and comprehensively represent the region’s spectrum of marine life characteristics, not just a subset of habitats or only species of special interest.

The focus on MPA networks recognizes the fact that a broad-area-integrated network that has been systematically developed and managed is often more effective than a series of small, highly protected areas surrounded by “a sea” of unmanaged activities.



Conservation and Marine Protection Areas, Figure 1 Map showing part of the GBRMP zoning plan.

| <b>GBRMP Zoning</b><br>(see relevant <i>Zoning Plans and Regulations</i> for details) |        | General Use Zone | Habitat Protection Zone | Conservation Park Zone | Buffer Zone | Scientific * Research Zone | Marine National Park Zone | Preservation Zone |
|---------------------------------------------------------------------------------------|--------|------------------|-------------------------|------------------------|-------------|----------------------------|---------------------------|-------------------|
| Aquaculture                                                                           | Permit | Permit           | Permit*                 | ×                      | ×           | ×                          | ×                         | ×                 |
| Bait netting                                                                          | ✓      | ✓                | ✓                       | ×                      | ×           | ×                          | ×                         | ×                 |
| Boating, diving, photography                                                          | ✓      | ✓                | ✓                       | ✓                      | ✓*          | ✓                          | ✓                         | ×                 |
| Crabbing (trapping)                                                                   | ✓      | ✓                | ✓*                      | ×                      | ×           | ×                          | ×                         | ×                 |
| Harvest fishing for aquarium fish, coral and beachworm                                | Permit | Permit           | Permit*                 | ×                      | ×           | ×                          | ×                         | ×                 |
| Harvest fishing for sea cucumber, trochus, tropical rock lobster                      | Permit | Permit           | ×                       | ×                      | ×           | ×                          | ×                         | ×                 |
| Limited collecting                                                                    | ✓*     | ✓*               | ✓*                      | ×                      | ×           | ×                          | ×                         | ×                 |
| Limited spearfishing (snorkel only)                                                   | ✓      | ✓                | ✓*                      | ×                      | ×           | ×                          | ×                         | ×                 |
| Line fishing                                                                          | ✓*     | ✓*               | ✓*                      | ×                      | ×           | ×                          | ×                         | ×                 |
| Netting (other than bait netting)                                                     | ✓      | ✓                | ×                       | ×                      | ×           | ×                          | ×                         | ×                 |
| Research (other than limited impact research)                                         | Permit | Permit           | Permit                  | Permit                 | Permit      | Permit                     | Permit                    | Permit            |
| Shipping (other than in a designated shipping area)                                   | ✓      | Permit           | Permit                  | Permit                 | Permit      | Permit                     | Permit                    | ×                 |
| Tourism programme                                                                     | Permit | Permit           | Permit                  | Permit                 | Permit      | Permit                     | Permit                    | ×                 |
| Traditional use of marine resources                                                   | ✓*     | ✓*               | ✓*                      | ✓*                     | ✓*          | ✓*                         | ✓*                        | ×                 |
| Trawling                                                                              | ✓      | ×                | ×                       | ×                      | ×           | ×                          | ×                         | ×                 |
| Trolling                                                                              | ✓*     | ✓*               | ✓*                      | ✓*                     | ×           | ×                          | ×                         | ×                 |

**PLEASE NOTE:** This guide provides an introduction to Zoning in the Great Barrier Reef Marine Park. Relevant Great Barrier Reef Marine Park Zoning Plans should be consulted for confirmation of use or entry requirements.

\* Additional restrictions / conditions apply.

**ACCESS TO ALL ZONES IS PERMITTED IN AN EMERGENCY.**

Conservation and Marine Protection Areas, Figure 2 GBRMP “activities matrix”.

### Tools for marine management

MPA managers generally do not manage natural systems or specific marine species *per se*; rather they manage the human impacts associated with those resources. Marine management is usually undertaken to achieve a desired set of goals and objectives; it is important that these goals and objectives are clearly established and widely known.

Ecosystem-based management and adaptive management are two key aspects of the effective management of any MPA, and these are particularly important because of the following:

1. The interconnectedness of different habitats of the marine environment and the interdependency upon neighboring biological communities;
2. The impacts from adjacent land or sea areas that may threaten the integrity of even the best managed MPA;
3. The three-dimensional aspects of what needs to be managed (few MPAs are well known, easily viewed, or easily “delineated” for management purposes, which means they are hard to see, hard to manage, and enforce). “Out-of-sight, out-of-mind” is part of the problem;



4. Ownership issues (for most marine areas worldwide, open-access resources are poorly or insufficiently regulated).

When used in the context of the above management and planning approaches, the following management tools are widely used by MPA managers:

*Zoning* – Spatial allocation using zoning is an accepted practice within many MPAs around the world. Zoning can separate conflicting uses and provide for high levels of protection for specific areas while allowing a variety of uses, including fishing, to continue in other zones.

*Permits and licensing* – When used in conjunction with a zoning plan and other management tools, permits, and licences can:

- (a) further regulate use in high-use or sensitive areas;
- (b) encourage responsible behavior in users and assist in monitoring activities; and
- (c) require the collection of data for planning and management.

Certain permit applications may also trigger the need for a comprehensive environmental impact assessment to be undertaken.

*Enforcement and surveillance* – Without an effective compliance and enforcement program, an MPA will not achieve its objectives. In time, its regulations will neither be accepted nor complied with by users or locals. Implementation and enforcement of regulations may include checking locations, size restrictions, bag limits, fishing season, or gear type, and can protect habitats, by-catch species, and spawning stock.

Enforcement and compliance can be very expensive because of the costs of resources, including trained personnel and access to appropriate vessels, aircraft, or specialist equipment. Enforcement should not, however, be considered as the only management approach or the tool of last resort.

*Public education and community engagement* – These are both integral to effective marine management. Communicators must build awareness of the threats and instil an acceptance for change. Effective public education and enlisting the assistance of key stakeholder groups, combined with enforcement and compliance, can result in valuable outcomes.

*Research and monitoring* – Research and monitoring can help MPA managers to diagnose problems, prioritize and implement solutions, assess the results and effectiveness of management actions, and forecast future conditions. Having the best available information for decision making helps ensure effective marine management of an MPA.

The above are only some of the main management tools used in coral reef conservation; other spatial tools include plans of management, specific closures, or special management areas. Non-spatial management tools include effective legislation, advisory committees, industry partnerships, best practice guidelines, or user fees such as

the “Environmental Management Charge” applied in the GBRMP.

### Key lessons learnt

1. In most MPAs worldwide, there are real challenges in maintaining existing levels of marine management, let alone coping with rapidly escalating levels of use or increasingly complex issues, such as climate change. Finding the right balance between protection and sustainable use is essential, and issues like cumulative impacts are becoming increasingly important to address.
2. An integrated management framework is important for effective marine management. Without it, intersectoral conflicts, incompatible activities, and inefficient systems will prevail. Integration across use sectors, levels of government, and the land–sea boundary are all fundamental to effective ocean governance and marine conservation.
3. Manage at the ecosystem level, not for single species. Most fishery management efforts focused on managing a single target species have failed. The more appropriate and effective approach requires managing all components and ecological processes as part of ecosystem-based management.
4. Local communities and indigenous people should be involved in marine management; successful examples of effective conservation have comprised a combination of “top-down” approaches (through government working with appropriate agencies or organizations), combined with effective “bottom-up” input involving community engagement. Widespread public support is essential if marine conservation efforts are to be successful and sustainable.
5. Apply the precautionary principle. We will never know precisely how coral reef ecosystems function or how they will cope with pressures such as climate change. But enough is known to cautiously proceed with management, comprehensively using the best available science and expert opinion (not waiting for perfect information) and adaptively managing as we continually learn.
6. Ensure that all MPA planning is open, transparent, collaborative, and adaptive, using the best available scientific, traditional, and local knowledge. Accommodate the economic, social, and cultural aspirations of communities within the ecological constraints.
7. Better technology can be a “double-edged sword” – while it may assist management (e.g., remote sensing, satellite imagery), it can also mean that users are able to access areas and resources that previously were inaccessible.

### What is the future for reef conservation?

As the global population increases markedly, the pressures on coral reefs are increasing significantly as are the difficulties in ensuring reef conservation. Regrettably, many

governments are not focused on long-term reef conservation outcomes, focusing more on short-term development issues or resource use; this means that matters such as long-term sustainability, adequate resourcing for relevant agencies, and funding for conservation are often of lower priority.

The conservation of the world's coral reefs is today at "cross-roads"; paraphrasing Kingsford et al. (2009)

1. In most areas, there is sufficient knowledge to implement effective policy, but effective implementation largely depends upon education, political will, community aspirations, and social and economic capacity;
2. As the knowledge of what is required for coral reef conservation has increased, so have the pressures; and
3. Proactive reef conservation measures that aim to build resilience to better cope with the likely pressures are considerably more cost efficient and are often less risky than waiting until the pressures have occurred and then trying to address them through reactive management.

## Websites

Great Barrier Reef Marine Park Authority <http://www.gbrmpa.gov.au>

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## Cross-references

*Acanthaster planci*

Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity

Climate Change: Impact On Coral Reef Coasts

Climate Change: Increasing Storm Activity

Climate Change and Coral Reefs

El Niño, La Niña, and ENSO

Engineering On Coral Reefs With Emphasis On Pacific Reefs

FORAM Index

Heavy Metal Accumulation in Scleractinian Corals

Impacts of Sediment on Coral Reefs

Infrastructure and Reef Islands

Mining/Quarrying of Coral Reefs

Nutrient Pollution/Eutrophication

Ocean Acidification, Effects on Calcification

Reefs at Risk: Map-Based Analyses of Threats to Coral Reefs

Temperature Change: Bleaching

Tsunami

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## COOK, JAMES (1728–1779)

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James Cook was the first of the great explorers of the eighteenth century to present a comprehensive account of the almost invisible reefs in the great open expanses of the Pacific Ocean. Intensified speculation had been mounting on such hazards to navigation when the destructive power of coral reefs was given sensational publicity in Cook's account of his successful discovery of the mysterious and elusive Great South Land, following the British scientific expedition in command of the *Endeavour* to Tahiti in 1769 for scientists to observe the Transit of Venus.

While subsequently exploring the unknown eastern coast of New Holland, on June 11, 1770, his ship crashed into one of the invisible reefs and the eventual discovery

of a way out of the bewildering complexity of the “labyrinth” of submerged reefs created a sensation. He published his description of the impact and the beaching of the vessel for repairs. Once safe in the ocean, Cook wrote one of the most powerful coral reef images ever: “A Reef such as is here spoke of is scarcely known in Europe, it is a wall of Coral Rock rising all most perpendicular out of the unfathomable Ocean... the large waves of the vast Ocean meeting with so sudden a resistance make a most terrible surf, breaking mountains high.”

In 1770, after his encounter with the Great Barrier Reef, Cook had become aware of a major scientific controversy among European and British naturalists that in some mysterious way coral reefs were built neither by rocks nor by petrified plants as 2,000 years of tradition had supposed, but were the production of microscopically small animals, then part of the extensive range of unknown, unclassified organisms collectively termed “insects”.

Barely 4 years later, during his second 1772–1775 exploratory voyage in the Pacific in command of the *Resolution*, as he navigated past continental islands in the central Pacific with elevated relict fringing reefs, he recorded in his *Journal* for June 1774 his puzzlement “If these Coral rocks were first formed in the Sea by animals, how came they thrown up, to such a height? Has this Island been raised by an Earth quake or has the sea receded from it? Some philosophers [scientists] have attempted to account for the formation of low isles such as are in this Sea, but I do not know of any thing has been said of high Islands or such as I have been speaking of,” thereby providing speculation for further reef research.

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## CORAL CAY CLASSIFICATION AND EVOLUTION

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### Definition

A coral cay is an island formed from sediments derived from the reef on which it sits and swept by refracted waves to a focal point on the reef flat where they are deposited. A cay initially may remain intertidal and lack vegetation, but with time it is likely to build up to be above sea level, acquire a vegetation cover, and become partially lithified.

### Introduction

Islands associated with coral reefs have been occupied or used by humans for millennia. They became known to western society as voyages of discovery crossed tropical waters. A distinction has been made between “high” islands composed of continental rocks and “low” islands of biogenic carbonate sediments produced by reef organisms. The variety of morphologies that were observed became a focus of early studies:

“There are different opinions amongst ingenious theorists, concerning the formation of such low islands”.

(James Cook, 17 April, 1777)

Scientific studies of reef islands were first made in the nineteenth century in south-east Asia and the Australian Great Barrier Reef (GBR) and subsequently in the Pacific and Indian Oceans and in the Caribbean Sea (see [Table 1](#); [Stoddart and Steers, 1977](#)) (see [Steers, James Alfred \(1899–1987\)](#); [Stoddart, David Ross \(1937–\)](#)).

As the diversity of form became evident, various attempts at classification were undertaken. More recently research has extended to understand processes that form and maintain coral cays and their origin, age, and evolution. Many of these investigations, especially the development of classifications, were based on studies of the GBR ([Spender, 1930](#); [Steers, 1929, 1938](#); [Fairbridge, 1950](#); [Stoddart and Steers, 1977](#); [Hopley, 1982, 1997](#); [Hopley et al., 2007](#)). The GBR is the largest reef province in the world, which when combined with the adjacent Torres Strait contains over 1,000 islands including approximately 350 coral cays ([Hopley et al., 2007](#)). Stretching over 15° of latitude and with reefs extending from the mainland to the shelf edge, the GBR provides a diversity of environments which are responsible for the great variety of coral cay types found within its waters (see entry: Section 10.1.3 in [Hopley et al., 2007](#)).

### Cay formation: wave influences

Coral cays generally occur on reef flats at or very close to sea level. The reef flat need not be large (many occur on small reefs <1 km<sup>2</sup>), and some sand cays in the Maldives have been shown to develop over lagoonal sediments while the reef flat is still evolving ([Kench et al., 2005](#)). A supply of biogenic sediments is fundamental for cay formation, but most reef tops have partial veneers of sand and shingle and there are many with diffuse sediment sheets that remain unconcentrated. The most critical factor for cay formation is the centripetal pattern of sediment movement produced by waves and currents in response to reef shape; centripetal sediment transport delivers sediment to a focal point or depositional node where it may accumulate (see [Hydrodynamics of Coral Reef Systems](#); [Wave Shoaling and Refraction](#); [Waves and Wave Driven Currents](#)).

Two related features of wave transformation over a reef control whether or not deposition is spatially concentrated. The first is the convergence of waves. The depth of water just beyond the reef front means that waves do not fully



Coral Cay Classification and Evolution, Table 1 Flora of reef islands

| Ocean              | Island(s)                             | No. | Or area              | Source                               | Total No. of sp. | % Indigenous |
|--------------------|---------------------------------------|-----|----------------------|--------------------------------------|------------------|--------------|
| Atlantic ocean     | Belize cays                           |     |                      | ARB256 (Stoddart et al. 1982)        | 178              | 82           |
|                    |                                       |     |                      | ARB258 (Fosberg et al. 1982)         |                  |              |
|                    | Cayman Island cays                    |     |                      | Sauer (1982)                         | 102              | 67.6         |
|                    | Glovers Reef <sup>a</sup>             | 6   |                      | ARB257 (Stoddart et al. 1982)        | 70               | n.a.         |
| Indian ocean       | Jamaican cays                         | 15  |                      | ARB351 (Stoddart and Fosberg 1991)   | 105              | 79.0         |
|                    | Cocos-Keeling <sup>a</sup>            | 22  |                      | ARB404 (Williams 1984)               | 130              | 46.9         |
|                    | Diego Garcia <sup>a</sup>             |     | 30 km <sup>2</sup>   | ARB313 (Topp 1988)                   | 191              | n.a.         |
|                    | Kavaratti <sup>a</sup> (Lacadives)    |     | 3.63 km <sup>2</sup> | ARB266 (Sivadas et al. 1983)         | 117              | n.a.         |
|                    | South Indian cays                     | 6   |                      | ARB161 (Stoddart and Fosberg 1972)   | 84               | n.a.         |
|                    | Winhingili <sup>a</sup> ; Addim atoll |     | 0.97 km <sup>2</sup> | ARB231 (Spicer et al. 1989)          | 72               | n.a.         |
|                    | Maldives                              |     |                      |                                      |                  |              |
| Pacific ocean      | Bikini <sup>a</sup>                   | 22  |                      | ARB315 (Fosberg 1988)                | 67               | 52.2         |
|                    | Kapingamarangi <sup>a</sup>           | 22  | 112 ha               | ARB362 (Woodroffe and Stoddart 1992) | 99               | 50.5         |
|                    | Nui <sup>a</sup>                      |     | 337 ha               | ARB362 (Woodroffe and Stoddart 1992) | 86               | 51.2         |
|                    | Ontong Java <sup>a</sup>              |     | 650 ha               | ARB362 (Woodroffe and Stoddart 1992) | 146              | 56.2         |
|                    | Suwarow <sup>a</sup>                  |     | 200 ha               | ARB362 (Woodroffe and Stoddart 1992) | 45               | 51.1         |
| Great Barrier Reef | Northern cays                         | 80  |                      | ARB348 (Fosberg and Stoddart 1991)   | 380              | 66.6         |
|                    | Bushy (Redbill)                       |     | 4.5 ha               | ARB350 (Walker et al. 1991)          | 34               | 82.3         |
|                    | Green                                 |     | 15 ha                |                                      | 114              | 47.4         |
|                    | Heron                                 |     | 19 ha                | ARB349 (Stoddart and Fosberg 1991)   | 51               | 49.0         |
|                    |                                       |     |                      | ARB440 (Rogers 1986)                 |                  |              |
|                    | Lady Musgrave                         |     | 13 ha                | ARB350 (Walker et al. 1991)          | 51               | 54.9         |

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<sup>a</sup>Atoll motus

refract and accommodate themselves to the reef front. Instead, around the reef perimeter except at the windward tip, they pass over the reef crest at a slight angle, leading to a zone of wave convergence toward the leeward reef flat. This is indicated clearly by the pattern of the aligned coral zone (see *Geomorphic Zonation*) on many reefs. However, centripetal transport and concentrated deposition are not developed on all reefs. Reef shape is critical, as it controls the pattern of refraction. Convergence of wave trains is most likely on oval reefs. However, interference of wave patterns by upwind reefs may mean that the waves approaching a reef are already refracted. In these circumstances, a clear focal point from further refraction may not be achieved, impeding island formation.

The second important feature of waves is their ability to transport sediment. Much wave energy is dissipated on the reef edge due to breaking and reflection. However, some energy is transmitted and smaller waves reform beyond the break point and move over the reef, where they are attenuated very slowly, unless water depths are exceptionally shallow or the bottom is very rough. The competency of reformed waves to move sediment is markedly diminished, even during major storms. Thus, coarse sediment is likely to be deposited on the windward margin where a shingle cay may form. Where waves tend to break normal to the reef front, this may be a rampart-like linear



Coral Cay Classification and Evolution, Figure 1 Windward shingle ridge parallel to reef front, Turtle 2 Reef GBR.

feature paralleling the reef crest (Figure 1; see *Shingle Ridges*). Alternatively, there may be sufficient refraction at the apex of a reef to concentrate coarser sediments into a compact island.

Generally, waves propagating over the reef flat beyond the rim are only competent to transport sands and finer sediments. As these waves slowly attenuate, sediments may be transported a considerable distance leeward.

Deposition occurs where refracted waves converge, either along the center of the reef or in a nodal area toward the lee. However, on very large reefs, waves that are distant from the reef front may become incompetent to transport even fine sediments that remain spread over the reef flat. Leeward sand cays thus form where there is both a centripetal convergence of refracted waves and sufficient wave power to transport sediments to a focal point. On large reef flats, sediment transport by refracted waves may be augmented by locally generated short-period wind waves, with their influence growing as rising tides increase fetch over broad reef platforms (Samosorn and Woodroffe, 2008). In high-energy areas and/or on smaller reef platforms, sediments may be swept entirely off the reef. Because maximum wave height over a reef flat is constrained by water depth (which is tidally modulated) and wave attenuation is a function of friction, a reef energy window index can be calculated from the ratio of the reef flat depth at mean spring high tide and reef width, which indicates potential geomorphic activity over a particular reef platform (Kench and Brander, 2006).

### Cay sediments

The textural characteristics of reef sediments play an important role in the bimodal distribution of reef flat sediment deposition observed on many reefs. Because shingle and rubble tend to break down into sands of approximately  $2\phi$  (Orme, 1977), a distinctly bimodal distribution of sediments and depositional environments develops under the wave-energy conditions described above (see *Sediments, Properties; Sediment Dynamics; Reef Flats*). Nonetheless, the basic division of reef islands into windward shingle cays and leeward sand cays is very much oversimplified.

Studies of GBR cays (Maxwell et al., 1961, 1964; McLean and Stoddart, 1978) suggest that for each cay type, either sand or shingle, sediments textures are remarkably uniform. McLean and Stoddart (1978) examined sediments of cays on the northern GBR and found that shingle is relatively homogeneous in composition (mainly *Acropora* clasts) but varies in size and shape, whereas sand cay sediments are mainly well-sorted ( $<1\phi$ ) medium to coarse sands ( $0-1.5\phi$ ) derived from a wider range of biota and are compositionally very similar to reef flat sediments. Where winds blow from one prevailing direction, the beaches on sand cays contain the coarsest sediments, particularly on the windward shore. Winnowing by the wind transports finer sand to the cay interior or berm, though dune structures are rare or poorly developed on most cays. McLean and Stoddart (1978) found that the finest sediments were associated with soils, either as a component of the active soil profile or within buried soil horizons.

The broad patterns established for GBR cay sediments are generally applicable elsewhere. Although sand cay sediments occur within a narrow textural range, small but distinct variations between cays develop due to

differences in proportions of constituent components (which may be related to the nature of the reef flat), differences in distances, modes, and rates of transport from source area to cay (dependent on the size of the reef and the location of the cay upon it), and variations in residence time since deposition. Coral cays may include minor amounts of siliciclastic sediment; pumice fragments floated in from volcanic source areas are common and can form distinctive strata up to 30 cm thick on some cays. Pumice fragments up to 0.5 m in diameter have been found, but more commonly they range between 1 and 5 cm in size. Occasionally, continental rocks reach cays in the roots of floating trees.

### Criteria used in classification

Several coral cay classification schemes have been proposed to accommodate and in some cases explain the variation in morphological and compositional diversity outlined above. Steers (1929) suggested three classes of reef islands based on his detailed work on the GBR in the 1920s and 1930s: sand cays, shingle cays, and low wooded islands. Spender (1930) proposed a general classification of reefs and low islands that recognized five classes of reef, four of which support reef islands (1) a sand cay; (2) a sand cay and unvegetated rampart; (3) a sand cay and vegetated rampart without extensive mangroves across the reef platform; and (4) a sand cay, vegetated rampart, and mangrove-forested reef flat. Spender referred to this latter class as “island reefs” but they are synonymous with Steers’s low wooded islands by which they are better known today (see *Low Wooded Islands*).

Fairbridge (1950) identified five classes of island based on sediment type, vegetation cover, and the occurrence of emergent reef flat – a function generally of late Holocene relative sea-level history that can vary geographically (Hopley et al., 2007). Fairbridge’s cay classes were (1) unvegetated sand cays; (2) vegetated sand cays; (3) shingle cay, with or without vegetation; (4) sand cay with shingle ramparts, vegetated or unvegetated islands and with mangrove swamp over reef top; and (5) island with exposed platform of older emergent reef, sometimes fringed by more recently deposited sediments. Hopley (1982, 1997) reviewed the literature on GBR reef islands and their classification and concluded that four criteria can be used to define a reef-island classification equally applicable to coral cays formed in other reef regions. The four key criteria that form the basis of reef-island classification are as follows:

*Criterion 1: Sediment type.* Sand, shingle, or a mixture of both can dominate reef islands. In areas of moderate energy and a prevailing wind direction, shingle is typically located toward the windward edge of the reef platform, and sand cays generally form near the leeward margin due to hydrodynamic sorting. This distinction may be less clear in areas rarely affected by storms where shingle deposits may be lacking or on reefs affected by frequent high-energy storms where successive ridges

of storm-deposited coarse material may form the island core, but are surrounded by a sandy beach (e.g., Lady Musgrave Island, southern GBR). Reef islands developed where wind direction seasonally reverses are also less likely to show the classic bimodal distribution of sediments, especially on smaller reef platforms where mixing is likely.

*Criterion 2: Island location on the reef platform.* Where sediments are available and the reef platform size and energy regime allow sorting to occur, shingle cays form near the windward reef margin and sand cays to leeward. On some platforms, reef islands may occupy a significant proportion of the reef flat; coral cays on lagoonal reefs within Maldivian atolls can occupy as much as 56% of the reef top (Kench et al., 2008). Where cays are large relative to the reef platforms on which they sit, it is difficult to define whether a cay is windward or leeward, as is also the case where cays are located centrally on the reef due to either seasonal wave climate reversals or a function of reef geometry.

*Criterion 3: Island shape.* Cay shape broadly falls between elongate and compact (oval to round). This trait is largely controlled by the interaction of reef shape and wave refraction and transformation around and across a reef. Compact islands form where sediment transport to a single focal node is most efficient. Therefore, the directional consistency and energy of the prevailing wave climate and the complicating effects of obstructions such as adjacent reefs on the transfer of this energy to the reef platform also influence island shape. Generally, but not always, compact cays are more stable than elongate cays; the ends of which can be particularly sensitive and move with small changes in wind and wave direction with a seasonal periodicity (e.g., Flood, 1986).

*Criterion 4: Vegetation cover.* Coral cays are either unvegetated or vegetated, with the extent of vegetation often reflecting island size, age, and stability. Climate, especially rainfall and frequency of storms, can also be important, but larger, older, and more stable islands generally possess better soils and groundwater aquifers best able to sustain vegetation. Reef-island vegetation is discussed further in Section Reef-island vegetation.

The four criteria above can be used to describe and classify reef islands that range from small and unstable unvegetated sandy cays to complex low wooded islands (see Section Classification: island types). It is important to note that two criteria – vegetation cover and island shape – may change abruptly, especially on reefs exposed to extreme events. For example, Pickersgill Cays on the GBR were reported as slightly vegetated by the Australian Pilot early in the twentieth century but unvegetated when Spender (1930) and Steers (1929) visited in 1929 and were again unvegetated in 1973 (Stoddart et al., 1978a). Rapid changes in reef-island morphology can be established by comparing aerial photographs or accurate GPS surveys at event and seasonal time scales, and these methods

commonly document significant shifts in shoreline at these short time scales (e.g., Frank and Jell, 2006). Historical maps available for some reef islands can be compared with later versions to show significant change over the past 50–100 years (e.g., Stoddart et al., 1978b; Flood, 1986). Relict beach rock outcrops indicate the position and shape of cay shorelines in the longer term past that can be very different to the present day morphology. Cay dynamics are covered in Section Factors influencing cay stability.

### Classification: island types

The main classes of coral cay are described in the following section. The defining features of major reef-island classes are depicted schematically in Figure 2.

#### Unvegetated cays

Unvegetated cays clearly lack vegetation. They are generally small and unstable; both conditions constrain the establishment and survival of plant cover. A mean area of just 0.5 ha was determined for 18 unvegetated cays surveyed in the 1973 northern GBR expedition (Stoddart et al., 1978a). They may be composed of sand and/or shingle and can be either elongate or compact. They are the most common cay type (see *Unvegetated Cays*).

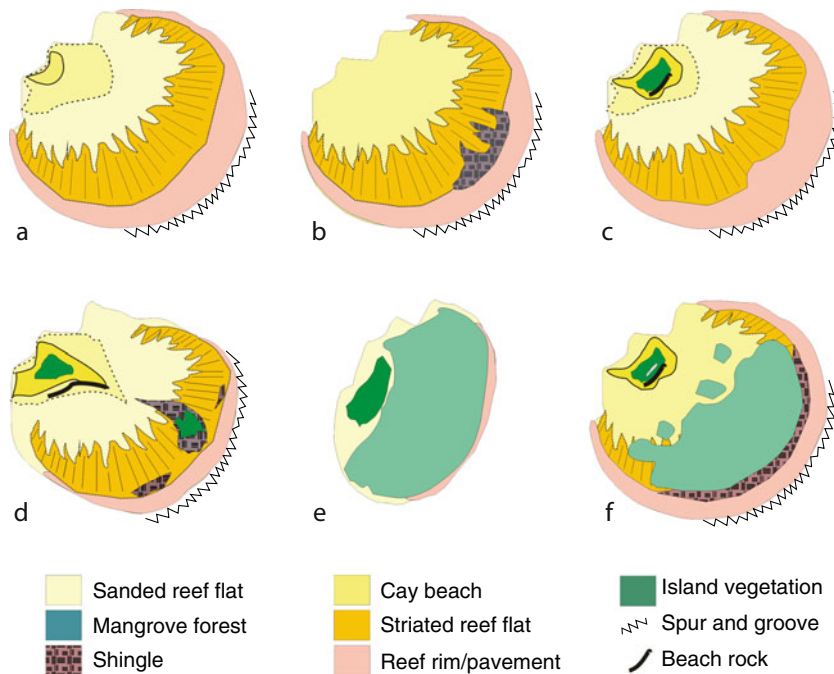
##### *Unvegetated sand cays*

Linear unvegetated sand cays form on medium to large planar reefs (see Chapter *Reef Classification by Hopley, (1982)*) of elongate shape where wave refraction generates opposing wave trains that meet along a central axis and where sediment accumulation takes place. Linear unvegetated cays may also form where winds seasonally reverse, producing an elongate, spit-like accumulation toward the leeward reef margin. Hopley (1982) considered that the migrating linear sand banks on the large planar reefs of Princess Charlotte Bay, northern GBR resulted from seasonal shifts between dominant south-easterly trade winds and lighter, more northerly monsoonal winds. Bidirectional monsoons have also been linked to the abundance of elongate unvegetated cays in Indonesia (Tomascik et al., 1997). Compact unvegetated cays form where strong centripetal sediment transport focuses deposition within a restricted locus (Figure 3a). Many are highly mobile and unstable (Hopley, 1978; Aston, 1995), especially the smaller (<0.1 ha) “ephemeral” cays that may be submerged at high tide (Figure 3a). Stoddart et al. (1982) concluded that many of these cays in the Caribbean, such as Paunch and Curlew Cay, may be second generation features reformed following the destruction of larger cays during storms. Larger unvegetated cays up to 400-m long and 120-m wide are often flanked by beach rock, suggesting greater stability.

##### *Unvegetated shingle cays*

Linear unvegetated shingle cays are very unstable reef islands, vulnerable to reworking and erosion near the reef front (Figures 2b and 3b). They are typically the product of





**Coral Cay Classification and Evolution, Figure 2** Schematic plan views of major reef-island classes: (a) unvegetated sand cay; (b) unvegetated shingle cay; (c) vegetated sand cay; (d) multiple island (with vegetated shingle island); (e) mangrove island (note no spurs and grooves as low-energy setting); (f) low wooded island.

high-energy storms and form as shingle ramparts coalesce. Unvegetated shingle cays can remain reasonably intact between storms, and cementation of basal sediments can occur, forming bassett edges (cemented lower parts of shingle ridges), which steeply dip away from the reef front (see *Bassett Edges*). However, bassett edges preserved after ramparts are eroded occur like outcrops of beach rock on many reef flats, suggesting that unvegetated shingle cays have also limited longevity (Hopley, 1982). Compact unvegetated shingle cays are generally restricted to small reefs, but vary from relatively mobile mounds of shingle and rubble through to complex structures with some degree of cementation.

### Vegetated cays

Eventually some unvegetated cays achieve sufficient stability for vegetation to successfully establish and this vegetation may confer additional stability (see Section Reef-island vegetation). As for unvegetated cays, vegetated cay sediments range from pure sand to shingle, and shapes range from linear to compact (see *Vegetated Cays*).

#### *Vegetated sand cays*

Vegetated cays are usually more stable than unvegetated cays, but can still change morphology and position. For example, in the Caribbean, Hurricane Hattie in 1961 completely removed St. George's East Cay that was 110-m long and 0.3 ha in size (Stoddart et al., 1982). Hopley (1982) argued that compact vegetated cays

(Figures 2c and 3c) are more stable than linear cays because (1) they usually have a proportionally larger vegetated area; (2) beach rock outcrops give better protection as they armor the beaches rather than become detached as on unvegetated cays; and (3) colonizing species tend to dominate linear cays for a longer period. Some vegetated cays are barely emergent at high tide, but others support dunes that rise several meters (Figure 3c). Beach rock can occur on the more stable long-axis flanks of compact and even linear vegetated cays, with massive outcrops exposed by subsequent erosion. For example, beach rock was absent from only one (Upolu Cay) of the 17 vegetated cays on the GBR mapped by Stoddart et al. (1978a). Flood (1977) also noted that beach rock was common on the 14 vegetated cays in the Bunker and Capricorn Groups he examined. Moderate though not necessarily extended stability is required for beach rock formation (see *Beach Rock*), and massive outcrops confer additional stability to a cay under erosive conditions. In contrast, spits at the ends of these islands are characteristically mobile and commonly shift from season to season. Mineralization of phosphates derived from guano has cemented sediments beneath the vegetation cover to form phosphate rock on some cays (e.g., Raine Island, GBR; Figure 7), also increasing island stability.

#### *Vegetated mixed sand and shingle cays*

Mixed sand and shingle cays may develop where wind direction shifts seasonally and shingle is supplied during



**Coral Cay Classification and Evolution, Figure 3** (a) Leeward unvegetated sand cay, Wheeler Reef, GBR. (b) Shingle cay with extended spit, Pandora Reef, GBR. (c) Vegetated sand cay, Bushy Island, Redbill Reef, GBR. Note: the zone of shrub vegetation fronting the interior *Pisonia* forest. (d) Tupai Atoll motus, French Society Islands. (e) Windward vegetated shingle island, showing constructional ridges and leeward vegetated sand cay, Fairfax Reef, southern GBR. (f) Low Isles, GBR, the classic low wooded island, site of the 1929 Royal Society Expedition.

one season and sand during the other (e.g., this process accounts for mixed sand and shingle cays in Torres Strait). Alternatively, shingle may be deposited during storms, with sand deposition during regular weather conditions. The latter mode appears to explain the sediment pattern of Lady Musgrave Island on the southern GBR. There,

shingle ridges have been episodically deposited by storm waves, with sand accumulating around the margins during normal trade wind weather. Mixed cays also develop where the character of sediments produced on the reef or delivered to the focal point of accumulation change through time, as may occur when reef geometry is modified or changing



sea levels modify reef flat hydrodynamics. In the atolls of the Caribbean, these mixed islands typically comprise a windward shingle ridge and leeward sand area. Lime and Hunting Cays are examples (Stoddart et al., 1982).

Reef islands deposited on atoll rims generally fall within this class, although the proportions of sand and shingle vary. On open-ocean atolls (see *Atolls*) in very low energy areas, e.g., close to the equator, islands may be predominantly sand but at latitudes where cyclones are more regularly experienced they tend to be dominated by shingle and boulders (see *Tropical Cyclone/Hurricane*). These linear shingle islands are generally larger than those found for example on barrier reef systems and are thus able to maintain a freshwater lens and diverse vegetation. Many of these islands have been home to Polynesian peoples for centuries or millennia and are commonly referred to as motu [Figure 3d; see *Atoll Islands (Motu)*].

#### *Vegetated shingle cays*

Vegetated shingle cays are uncommon. One Tree Island, Lady Elliot Island and East Hoskyn and Fairfax Islands (Figures 2d and 3e), all located at the southern end of the GBR, are among the few cays of this type to have been scientifically analyzed. However, Tomascik et al. (1997) suggest that they are probably common on the exposed parts of the Great Sunda Barrier in Indonesia. These cays typically develop near the windward margins of larger reef flats or centrally on smaller ones exposed to high energy. Most vegetated shingle cays are compact in form as linear shingle cays are usually either too narrow to retain adequate freshwater or too mobile for vegetation to endure. Where vegetation survives, the greater stability of the shingle cay allows vegetation succession to proceed until cyclonic disturbance occurs (Hopley, 1982). Observations from the atoll of Ontong-Java suggest that in areas of episodic high-energy storms and sufficient sediment supply, these cays may go through cycles of destruction, reformation, and revegetation (Bayliss-Smith, 1988). Stoddart et al. (1982) noted the mobility of these cays in the Caribbean, where substantial changes were recorded at North Spot and Rugged Cays between 1960 and 1972.

Hopley (1982) suggested that shingle cays developed from shingle ramparts, with the “tongues” of shingle and rubble that commonly trail leeward from ramparts also possibly involved; One Tree Island in the southern GBR has formed this way. The near concentric shingle ridges at Lady Elliot Island similarly document its formation over several millennia by the progradation of shingle ridges deposited during episodic storms (Chivas et al., 1986). However, as noted above, evidence from various locations suggests that storms may also destroy these features.

#### *Mangrove islands*

In low energy areas, mangroves may colonize reef flats (Figure 2e) and encourage sediment accumulation and island formation. Sediments deposited beneath the

mangroves vary from peats to carbonate mud. Mangrove islands are rare on the GBR, but are more common in Torres Strait (Hopley, 1997) where despite a relatively high-tide range mangroves more frequently develop in sheltered areas behind shingle ramparts. Similarly, reef top mangrove islands are reported from various locations in Indonesia without rampart protection but where low-energy conditions prevail due to proximity to the equator and associated benign wind regime [e.g., Pulu Panjang in the Berau Islands (Tomascik et al., 1997)]. They are common on reefs lacking windward ramparts in the Caribbean (Stoddart and Steers, 1977), but are generally restricted to high reef tops, areas of low energy, and areas of relatively low tidal range. Mangroves are common on the reefs of Belize and are associated with different types of island (Stoddart et al., 1982). “Mangrove cays” are mud mounds with a simple covering of mangroves: “Mangrove cays with dry sand areas” have featureless low lying sand areas within the mangroves; “Moat Islands resemble the low wooded islands of the GBR; and “Mangrove range” are complex and extensive arrays of mangroves with intermittent sand ridges especially on the windward side (see also Woodroffe, 1995). Mangroves are also common in sheltered locations within the three offshore atolls (e.g., Murray et al., 1999). In Florida Bay, mangrove islands began to accrete as the shallow Miami Limestone was flooded in the late transgression, with various models proposed to explain the location and processes of formation. Recent geochronological and lithological investigations suggest net accumulation punctuated by erosion episodes over the past few thousand years as the rate of relative sea-level rise slowed to its present position (Oches et al., 2009) (see *Mangrove Islands*).

#### *Multiple islands*

Multiple vegetated islands on a single reef are rare on the GBR; there are just two long-standing examples – Fairfax (Figure 3e) and Hoskyn Islands in the Bunker Group. Each includes both a vegetated shingle and vegetated sand cay on a single reef platform, shingle cay to windward, and sand cay to leeward (Figure 2d). On large reefs subject to seasonal reversal of winds but only rare storms, sand cays may develop at opposite ends of the platform; this appears to be the case at Masig-Kodall (Yorke Island) in Torres Strait (9°45'S) where seasonally reversed waves interacting with an unusually shaped reef produces two depositional nodes and islands. The same process is probably responsible for the occurrence of multiple islands in the Indonesian Archipelago, where according to Tomascik et al. (1997, p. 819) they are “not a rare occurrence.”

#### *Low wooded islands*

The basic pattern of a low wooded island comprises a windward shingle cay, a leeward sand cay, and significant mangrove development over the intervening reef top (Hopley, 1997; Figures 2f and 3f; see *Low Wooded Islands*). This combination of features may occupy



a great proportion of the reef top, usually between 25 and 50% but up to as much as 75% (Stoddart et al., 1978a). The majority of “classic” low wooded islands on the GBR occur on relatively small planar reefs on the inner shelf (e.g., Low Wooded Island – 87.9 ha), but they can occur on larger reefs (e.g., West Hope Island – 315 ha) (Stoddart et al., 1978a). Shingle ramparts that grade upward from the reef flat and have steep leeward faces are encountered at varying distances from the windward margin. These ramparts frequently parallel the reef edge, but shingle tongues may trail toward the reef interior (see *Shingle Ridges*). Mangrove stands develop in the relatively protected area behind the shingle ramparts and may eventually expand to cover much of the reef flat. The degree of mangrove colonization was considered to reflect the stage of island development by some workers (Steers, 1937; Fairbridge and Teichert, 1947), but others contend the degree of protection afforded by windward structures is responsible (Stoddart et al., 1978c; 1982). Stoddart (1980) suggested that once the protection is provided, the extent and rate of spread of reef top mangroves varies markedly between reefs, and the mangroves are in fact opportunistic colonizers. Organic muds occur beneath the mangroves on some islands but elsewhere the mangroves grow over sandy reef flats. Fields of emergent fossil microatolls document the higher mid-Holocene sea level and later regression experienced by the planar reefs on which low wooded islands on the GBR have formed (McLean et al., 1978; Chappell et al., 1983) (see *Mid-Holocene*).

The leeward sandy cays are morphologically diverse. Some are small, ephemeral, and unvegetated but larger vegetated cays replete with terraced morphology also occur (e.g., Ingram Island). The characteristic complexity of low wooded islands ensures that they are a heterogeneous group. Stoddart et al. (1978a) distinguished four low wooded island types, *low wooded island with limited reef top mangroves and a separate sand cay* are most numerous. *Low wooded island with reef top mangroves extending between windward shingle and leeward sand cays* are also common, with Bewick Island on the northern GBR the type-example. “Turtle-type” low wooded islands lack the central reef flat, with shingle ramparts and conglomerates extending to the leeward cays (Figure 1). They are generally restricted to small reef platforms (<60 ha) where they occupy a large proportion of the reef flat. The final class described by Stoddart et al. (1978a) includes those that could not be assigned to the groups above. Hannah Island, a sand cay completely encircled by mangroves, provides an example.

A chronology for reef flat formation and low wooded island accretion on the GBR has been established by radiocarbon dating (see Hopley et al., 2007 for summary). The dates suggest that (1) many low wooded islands formed under higher sea-level conditions prior to 3,000 years ago; (2) there is no consistent pattern in the timing and order of shingle and sand cay development on different reefs; and (3) many low wooded islands were in place

or substantially developed by the mid-Holocene and exist in similar form today, suggesting stability in the longer term. However, comparison of the detailed maps of Low Isles and Three Isles in 1928–1929 (Spender, 1930) with those produced later show modifications to ramparts, mangroves and cays, indicating that change may be constantly taking place (Stoddart et al., 1978b; Frank and Jell, 2006). Although the most detailed descriptions of these islands come from the inner northern GBR, equivalents occur in other reef provinces and include Salt and Pigeon Cays in Jamaica, and the Snake Cays in Belize, where they are referred to as “moat islands.”

### Reef-island vegetation

Vegetation plays an important role in the evolution of coral cays, being integral to all classification schemes, and showing important changes through time (see *Coral Cays, Vegetational Succession*). Progressive accretion is expressed by “rings” of vegetation from low creepers and grasses growing on recently deposited carbonate sands immediately behind the beach, through a zone of shrub vegetation on young soils with minor organic content, to an internal climax vegetation of woodland or forest growing on mature soils (see *Soils of Low Elevation Coral Structures*; Figures 3c and 4). The vegetation itself, together with the developing soils contributes to stability. Erosional episodes with subsequent return to progradation may result in the shrub or woodland vegetation being exposed immediately behind the beach or with a new area of colonizing vegetation fronting the climax vegetation.

The initial establishment of vegetation and subsequent changes has a number of requirements. Colonizing vegetation requires a degree of stability and access to some rainfall or brackish water (Figure 5). Addition of organic matter to the raw carbonate sediments comes not only from the vegetation but also from bird guano as nesting and roosting birds become attracted to the cay. As noted,



**Coral Cay Classification and Evolution, Figure 4** Climax forest vegetation dominated by *Ficus benghalensis*, Soneva Fushi, Maldives.



**Coral Cay Classification and Evolution, Figure 5** Pioneering creeper vegetation, pantropical *Ipomea pes-caprae*, Rodrigues Island, Indian Ocean.

the presence of phosphatic cay sandstone (Figure 7) is indicative of mature vegetation and is an obvious source of nutrients for the higher plants (see *Phosphatic Cay Sandstone*).

The origin of the vegetation on islands that may be hundreds or even thousands of kilometers from continents or other coral islands and the structured similarity of the cay vegetation worldwide were enigmatic to early explorers and naturalists. However, it soon became apparent that the seeds of many of the plants float and reach remote shores via ocean currents. Other seeds are ingested by birds and excreted on the island, or attached to plumage, sometimes causing the mortality of the bird. In both cases, the seeds are deposited with an organic fertilizer. More recently, exotic plants have been brought to islands by early settlers (e.g., Polynesian voyagers) and in some instances became dominant over the original preexisting vegetation. However, the harsh environment of coral cays with strong environmental influences such as climate, water availability, soil, and nutrient limitations enforces pantropical controls on the success or otherwise of cay plants and is the ultimate reason for the structural similarity of coral cay vegetation worldwide.

Physiognomic similarities conceal what is a very complex flora. For example, atolls thousands of kilometers into the Pacific and Indian Oceans have plant lists ranging up to almost 300 species [Table 1; e.g., Kiribati, 290 species (Thaman, 1987)], even though nearly all coral cays and low reef islands are less than 6,000 years old. Also in spite of the isolation of many reef islands, they have very few endemic plants. The number of plant species is dependent on:

- (a) Island size (even for isolated atoll motus, this is an important factor)
- (b) Remoteness from other islands or most importantly continental land masses

- (c) The period of human occupation (and introduction of exotics)
- (d) The frequency of disturbances which can range from natural events such as cyclones or tsunamis to human disruptions for coconut plantations or nuclear weapon testing

Dispersal distance from other land masses may not be based on present geography, but instead could reflect land configuration and the distribution of island “stepping stones” present during glacial low sea levels. For example, on the northern GBR at the maximum of the last glacial the whole continental shelf was dry and mainland carbonate dominated shorelines would have stretched, for example, across the Gulf of Papua allowing the retention of a wide range of plants currently found on the cays. Present day reefs that are further off shore would, at that time, have been high limestone islands and whilst, for a short period, they may have been little or no land in the form of islands on the continental shelf, as reefs were initially drowned by the post glacial sea level (see *Holocene High Energy Window*), the nearby mainland would have been a permanent source of floating seeds carried out to the offshore evolving cays. Today, the islands of this area have 380 species of plants (Fosberg and Stoddart, 1991). In contrast, the reefs and islands of the southern GBR would have remained isolated from continental Australia, even at the maximum low sea-level stage. Today, these islands (the Bunker-Capricorn Group) support only 80 species, between 22 and 40 on individual islands (Stoddart and Fosberg, 1991).

The range of substrate types is also important in determining the number of species present on an island. Sand and shingle substrates have contrasting species lists but these are expanded if different types of cemented substrate such as conglomerate or phosphatic cay sandstone occur. This was one of the conclusions of Sauer (1982) in his comprehensive review of vegetation on the Cayman Islands with a focus on the unconsolidated carbonate sediments, the vegetation of which is equivalent to that of Caribbean cays. His conclusions are applicable across other Atlantic and Indo-Pacific reef islands.

Sauer noted the importance of introduced species that can contribute 50% of cay flora (Table 1). Indigenous cay flora have very poor defensive mechanisms and are easily displaced. For example, on Mopelia atoll in the Society Islands, 50 of 85 species are introductions (Sachet, 1983). However, introduced species, unless cultivated, can also quickly disappear. During World War II, 129 species were introduced to Canton atoll, but by 1973 only 14 persisted. Sauer also examined the distribution of coral island plants, noting that while endemics were few, the flora of Atlantic islands had many commonalities as did that of the Indo-Pacific. There is also a distinctive pantropical element. The best known of these is the coconut tree, *Cocos nucifera*, but away from its source area of South-east Asia, it is an introduction on most islands. Pantropical species are mostly dispersed as float seeds with the ability

to remain viable for at least 6 months. More often than not these pantropical species are part of the initial beachfront colonizing vegetation (Figure 5). Sauer (1982) noted 11 pantropical species on the Caymans, but many more occur in the Pacific. For example, of the 380 species listed for the northern GBR (Fosberg and Stoddart, 1991), 25 also grow on the Cayman Islands though a number may be introductions. Twenty-seven GBR species were also found on Jamaican cays (Stoddart and Fosberg, 1991) and 33 on the cays of Belize (Fosberg et al., 1982).

Many questions remain unanswered about coral cay vegetation. Although apparently simple, with a classic pattern of ecological succession, the highly successful mechanisms of dispersal reinforce at the species level, the global physiognomic similarities. However, even this ability does not answer all questions. As Sauer (1982) noted, the fossil record for this vegetation is very poor, though clearly going back until at least the Tertiary. It has thus become involved in plate tectonics and changes to global land masses, especially the isthmus of Panama, which now closes the link between Caribbean and the Indo-Pacific. While there are possibilities of some flora migrating around the southern tip of Africa, this would entail a long route outside the tropics. Today's pantropical species may be the last vestige of the more open Tertiary geography of meso-America.

### Age, evolution, and relationships to Holocene sea level

A foundation, usually a reef flat at or near to sea level, is necessary for reef-island formation, but it may be small and not yet sea level constrained (Hopley, 1997; Kench et al. 2005). The relationship between reef growth, sea level, and reef flat formation on a global scale is complicated by various factors including postglacial isostatic adjustments of the continents and ocean basins, which have produced broad geographic differences in relative sea-level history and especially when reef tops first approached the sea surface (Clark et al., 1978; Lambeck et al., 2002). Pirazzoli (1991) presents detail on these patterns (see *Glacio-Hydro Isostasy*), but the relative sea-level curves for most of the Pacific and the Caribbean and thus the potential onset of cay formation in these two provinces are very different. Modern sea level in the former was reached 6,000–5,000 years ago, in places rose 1–2 m higher and has then fallen to present, whereas in the Caribbean it has been rising throughout the Holocene but, slowing over the past few thousand years. Modern sea level has only recently been reached (Toscano and Macintyre, 2003). Further, at a more regional scale, isostatic influences driven by differential loading by postglacial transgressive seas can produce variable relative sea-level histories as deeper shelf edge areas subside under water load (delaying reef flat formation) and shallower inshore areas possibly upwarp (Hopley, 1983; Lambeck and Nakada, 1990). Other factors that influence when a reef reaches sea level and provides a base for

reef-island development include the depth from which the reef has grown and the size of the reef and its lagoon. Typically, reef islands are oldest where current sea level was reached early – in the mid-Holocene, where the reefs grew from shallow substrates and were thus sea level constrained earlier, and where they grew on relatively small reefs with smaller lagoons that were infilled more rapidly than those of larger reefs.

The relationships described above are demonstrated on the GBR, where stable vegetated cays are strongly associated with planar reefs; 41 of 43 are on planar reefs that grow above shallow pre-Holocene foundations (mean: 10.8 m) and are relatively small (mean: 4.1 km<sup>2</sup>). Planar reefs also have the oldest mean reef top age (~6,000 years), so that depending on where reef geometry and hydrodynamic conditions initially focus sediment deposition, cay formation could have begun 6,000 years ago (Hopley et al., 2007). In Hopley's (1982) evolutionary classification of reefs [see *Reef Classification*, Hopley (1982)], planar reefs represent a senile stage approaching the end of their growth trajectories. Significantly, most reef islands with any degree of permanence are found on these senile reefs though at the time of their initiation the reef could have been at an earlier state (even reef patches) and persisted through the mid to late Holocene period of lagoon infilling and reef flat extension. Thus, at the geological time scale the factors that promote the advance of reefs through the reef growth sequence are also important drivers of cay formation. Spender's (1930) hypothesis that reef-island formation is strongly influenced by relative sea-level fall and reef platform emergence was dismissed for more than five decades (Steers, 1937; Stoddart, 1965). However, the importance of hydroisostatic upwarping of the inner shelf in accelerating the development of reefs to planar stage and as a consequence improving reef-island accumulation and, possibly, preservation is now generally accepted for the GBR.

Most reef islands on the GBR and all low wooded islands are inside the zero hydroisostatic isobase. Emergent reef occurs beneath reef islands in many other settings (discussed below). Kench et al. (2005) suggested that some Maldivian cays began to develop prior to reef flat formation, and West Indian cays have formed where sea level has risen gradually to present since the mid-Holocene (Woodroffe, 2003). Radiocarbon-dated fossil microatolls underlie many of the reef islands which have been investigated on the GBR, suggesting that most of them developed after the reefs had reached sea level (see Hopley et al., 2007 chapter 10), but the occurrence of ~75 unvegetated cays on platforms close to sea level suggests that emergent reef platforms are not absolutely necessary. Reef islands on the Cocos (Keeling) Islands, Indian Ocean are also deposited over fossil reef flat that are made emergent by the falling late-Holocene sea levels (Woodroffe et al., 1999). Dickinson (2004) revisited the earlier ideas of Schofield (1977) and proposed that wave-resistant emergent palaeoreef flats strongly influenced the development of stable reef islands on many Pacific atolls,



but he acknowledged that less stable “unpinned” reef islands are common on reef flats that remain flooded by lower tides. These higher foundations that confer stability to overlying islands are not always composed of Holocene reef. Cays composed of or attached to Pleistocene reefal deposits, or occasionally eolianites (see *Eolianite*), are common in the Bahamas and offshore from British Honduras (Milliman, 1973).

Establishing precise chronologies for reef-island formation is difficult as radiocarbon dates age the death of the contributing organism and not the age of the deposit; in many settings, these two ages can be centuries or even millennia apart. If the radiocarbon chronologies are correct, rapid sand production, delivery, and cay deposition occurred on many planar reefs of the GBR between 4,000 and 3,000 years ago, with only relatively minor modifications since. Similar histories are reported from elsewhere (Kench et al., 2005; see Woodroffe, 2008), including for Warraber in Torres Strait where bulk sand ages suggest a growth chronology very similar to those of the GBR cays described above. However, AMS radiocarbon dating of specific skeletal components suggests that the mid-Holocene age may be an artifact of age determination on bulk sands; ages of molluscs indicate sustained incremental accretion of Warraber over the past 3,000 years (Woodroffe et al., 2007). This pattern of incremental development is observed on many reef islands across the Indo-Pacific, rather than rapid deposition in discrete periods or phases (Woodroffe, 2008). It is important to note that progressive sea-level change and island growth may modify sediment production, transport efficiency over the reef platform, and depositional nodes. For example, where sea level has fallen during the late Holocene, reduced reef flat depths may significantly reduce sediment delivery to leeward cays (Kench and Brander, 2006).

The central, oldest areas of cays may be indicated by the presence of mature vegetation and greater soil development (see previous section), although Woodroffe and Morrison (2001) found no clear relationship between soil development and age at Makin Island, Kiribati. Reef-island formation has not ceased, and new reef islands will form if reef growth and sediment production continues. Hopley et al. (2007) present average estimates of the time required to progress through this sequence on the GBR and emphasize that small shallow lagoonal reefs can transform into planar reefs in as few as 250 years. Thus, where sediment supply is adequate and reefs of suitable elevation, geometry, and energy exposure exist, reef islands may form quite rapidly.

### Factors influencing cay stability

There are many records of cays, including those with a mature vegetation cover, disappearing completely, both during storms and over longer periods of time. Lines of beach rock on numerous reef flats attest to the previous presence of a cay even where there may be no historical record. A number of factors are involved which may also

require consideration when assessing the future impacts of global climate change. For the 300 reef islands of all types found within the Great Barrier Reef Marine Park, Aston (1995) carried out a statistical analysis of the factors that contributed to stability. They varied with island type but included:

- (a) *Location on reef flat and size of reef.* The position of the cay on the reef flat is determined by wave refraction patterns, which on most small to moderate size reefs is toward the lee side. On large reefs and irregularly shaped reefs, the area of sand delivery may be less focused and broad areas of sediment deposition in the central reef flat may result. Any cay that forms will be highly mobile as small weather changes result in contrasting wave refraction patterns.
- (b) *Size of cay.* Reef islands may vary from a few tens of meters in diameter, to several kilometers. As it takes a considerable period for large bodies of sediment to accumulate, the larger islands are indicative of stability, requiring major changes in energy conditions to produce significant changes to the cay shoreline.
- (c) *Shape of cay.* Cays vary from oval to elongate. Oval cays represent a sediment body that has been constructed by the same energy conditions over a period of time and are the most stable. Linear cays, often with highly mobile spits on both ends, are by far the least stable with location and orientation of the spits often changing seasonally especially in monsoonal climates (Figure 8).
- (d) *Vegetation.* A degree of stability is required for a mature vegetation to take hold on sand cays. Very important is the availability of a freshwater lens associated with cays with a minimum width of ~120 m (see *Coral Cays – Geohydrology*). Vegetation is not only indicative of at least some degree of stability but also through the binding action of roots, the addition of organic matter to soils and protection from heavy tropical storms by the canopy, it adds further to the island stabilization process.
- (e) *Cementation.* Several cementation processes produce hard rock outcrops which retard erosion. Intertidally beach rock can form very quickly (Figure 6). Similar intertidal cementation can occur on shingle islands forming conglomerate outcrops. On older islands, which have had a mature vegetation for some time and which have been used as nesting or roosting sites for sea birds, the leaching of guano into the soil can result in the formation of phosphatic cay sandstone (Figure 7) at the water table.
- (f) *Sediment budgets.* Over time the delivery of sediments to the reef flat, and ultimately to the reef cay, can change. Initially when the reef first reaches sea level, its high proportion of coral cover may be producing calcium carbonate at rates up to  $10 \text{ kg/m}^2/\text{yr}^{-1}$ , though much of this goes into the infilling of irregularities in the maturing reef flat. Ultimately, the reef flat may become totally sediment covered with delivery of



**Coral Cay Classification and Evolution, Figure 6** Massive beachrock, so important for cay stability, Wilson Island, southern GBR.



**Coral Cay Classification and Evolution, Figure 7** Phosphatic cay sandstone formed from the leaching of guano, Raine Island, northern GBR.

sediment to the cay during this period of change declining significantly. This may be due to a reduction in the ability of waves to transport sediment to a focal point (see *Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity*) or to the stabilizing effect of reef flat sea grass or macroalgae (e.g., at Green Island GBR where eutrophication in the 1950s and 1960s caused an expansion of sea grass on the adjacent reef flat which prevented delivery of sand to the cay, see Hopley, 1982, pp. 333–335. Erosion of the cay has taken place subsequently).

- (g) *Platform height*. A fall in relative sea level since a cay first formed (due to hydroisostatic or other causes) can leave a cay “perched” on its reef flat. The effect is to greatly reduce the power of waves to deliver sediment which is now limited to only a small part of the tidal cycle. An erosional phase may result though a rise in

sea level may have the opposite effect (see *Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity*). Kench and Brander (2006) give some Australian examples.

- (h) *Meteorological conditions*. Cay location and morphology are strongly influenced by ambient weather conditions including storms which occur on a regular basis, producing short-term cycles of erosion and aggradation. However, there are many examples of changing wind strengths and direction causing longer term changes to reef islands as wave refraction patterns across the reef flat are modified and the orientation of an island changes or its location is changed so that it now loses sand over the reef edge (see Hopley et al., 2007, Chapter 13.5.3).

### Coral cay dynamics

Coral cays, composed of largely unconsolidated sediments, are classic natural systems in a state of dynamic equilibrium. Any change to the cay formation process – weather conditions, sediment budgets, reef morphology, or ecology – will produce an immediate response in the cay. Sediments are easily moved and high-energy events such as storms or tsunamis can produce major changes. However, small but significant changes are constantly taking place, over single tidal cycles, seasonally, over periods of years to decades in response to climate fluctuations, or in response to high-energy events. Each of these time scales is examined below with the majority of examples coming from the GBR where many islands of all types have been the subject of monitoring programs and a comparative study of all 300 islands within the Marine Park has been undertaken (Aston, 1995).

- (a) Tidal cycle changes

Hopley (1981, 1982) measured beach profiles around islands and sediment movement on the adjacent reef flat using sediment traps (Hopley, 1981) at three contrasting sites on the GBR over periods of high spring tides of up to 5 days. The sites were at Wheeler cay (a small unvegetated sand cay) (Figure 3a), Bushy Island (a maturely vegetated cay with *Pisonia* forest) (Figure 3c), and Three Isles cay (the leeward vegetated sand cay of a major low wooded island). Results were much as expected, with the largest changes to the beach and greatest sediment movement on the adjacent reef at unvegetated Wheeler Reef and smallest at the partially protected low wooded island site of Three Isles cay (Table 2).

- (b) Seasonal changes

Monsoonal climates produce significant changes to coral cays. This is illustrated by Coconut (Poruma) Island in Torres Strait, a narrow island of about 40 ha (Figure 8). Bi-monthly surveys at 21 sites in 1996–1997 recorded great mobility in the terminal spits with an annual pattern of erosion during the summer north-westerly monsoon, but with a return of

sediment from the reef flat under the influences of the winter south-easterlies. However, this cay is close to the reef edge and a circulatory movement of sediment around the island does produce a small net loss of sand of about 20,000 m<sup>3</sup>, equivalent to about 1% of the island volume (Hopley and Rasmussen, 1998).

Cays of the Maldives are also under strong monsoonal influence with large gross changes (31–21% of beach area) in shoreline position between seasons,

reflecting significant reversals in sediment flux of  $9\text{--}23 \times 10^3 \text{ m}^3$  biannually (Kench and Brander, 2006). However, annual net change is small (2–15%) indicating the island is in dynamic equilibrium.

(c) Decadal changes

Longer term surveys from aerial photography and ground truthing can determine if there is a long-term trend in cay changes and the dimensions of these changes. On Raine Island (northern GBR), Gourlay and Hacker (1991) reported erosion of up to 20 m and accretion of up to 40 m between 1967 and 1990 at specific points around the shore as the cay became more elongate. Annual sand movement on this small vegetated cay was about 5,000 m<sup>3</sup>. On Warraber in Torres Strait, maximum net shoreline movements over a 20-year period were around 60 m and at Green Island near Cairns, about 50 m between 1945 and 1978 (see Hopley, 1982). In the Bunker-Capricorn Islands, Flood (1988) measured average shoreline movements of between 14 and 53 m between 1972 and 1986 with maximum changes of up to 116 m.

These decadal changes include responses to specific cyclonic events, but also reflect long-term variations to weather patterns. In Torres Strait, wind records between 1951 and 1992 show a statistically significant increase in winter winds from the south-east, and an increase in wind speed at about 1975–1977. Realignment and a change in shape has occurred on some cays. Similar changes took place in the Bunker-Capricorn Islands. Here the annual wind energy vector has oscillated within a 45° arc from south-south-east in the early 1960s to east-south-east

**Coral Cay Classification and Evolution, Table 2** Contrasting beach changes, reef-flat sediment movement, and cay migration: Wheeler Cay (unvegetated); Bushy Island (mature vegetated); and Three Isles (low wooded island cay)

|                                                            | Wheeler Cay | Bushy Island | Three Isles |
|------------------------------------------------------------|-------------|--------------|-------------|
| Range of mean wind speeds (ms <sup>-1</sup> )              | 2.0–7.5     | 2.5–10.5     | 7.5–13.0    |
| Mean daily beach change (cm)                               | 17.46       | 2.74         | 1.51        |
| Maximum mean daily beach change (cm)                       | 24.95       | 2.76         | 1.98        |
| Mean daily sediment trap recovery (g)                      | 531.1       | 204.2        | 22.8        |
| Maximum mean daily sediment trap recovery (g) <sup>a</sup> | 793.1       | 344.4        | 39.7        |
| Recorded long-term migration (m)                           | 110         | ~40          | ~35         |
| Period                                                     | 1975–77     | 1936–74      | 1929–73     |

<sup>a</sup>This is the maximum mean recovery from all traps set. Individual traps have recorded up to 4,063 g on a single day on Wheeler Cay.



**Coral Cay Classification and Evolution, Figure 8** Seasonal fluctuations in shoreline position, Poruma Island, Torres Strait.



in the 1970s, sufficient to cause some of the shoreline changes experienced during this period (Flood, 1986).

(d) High-energy, low-frequency events

Cyclonic events can cause erosion or accretion on reef islands depending on the tidal conditions and sediment availability at time of impact. If tides are high, erosion usually results; if low, then accretion may occur (Flood, 1986). Storm surges that exacerbate erosion on mainland sites have far less an impact on cays on offshore reefs, which generally lack the gradual shoaling of mainland bays and the funneling effect of coastal embayments. Many examples have been described from the GBR (Flood, 1980, 1981, 1986; Flood and Jell, 1977; Hopley, 1972). Cyclone Emily (1972) with a central pressure of 985 hPa produced surge levels >2 m on the Queensland mainland near Gladstone, but only 0.8 m as it passed over offshore Heron Island (Hopley, 1972). On nearby One Tree Reef, around 27 m of rubble was added to the ramparts on the southeast side of the island as this cyclone struck at low tide. In contrast, Cyclone Winifred (982 hPa) in 1986 passed over Green Island at high tide producing 70 m of erosion on the unstable spit. At low latitudes where the Coriolis force is insufficient to generate mature cyclones, swell waves from cyclones at slightly higher latitudes can still affect island shores.

Tsunamis can be experienced in many reefal areas. The 2004 Indian Ocean event (see *Tsunami*) caused washovers in several island groups (e.g., Maldives, Chagos) and although leaving erosional scars of up to 2 m and depositional sand sheets extending inland, the overall geomorphological impact was not as great as might have been expected.

All of these natural changes can be exacerbated by anthropogenic activities (see *Infrastructure and Reef Islands; Engineering on Coral Reefs with Emphasis on Pacific Reefs*). Groynes, rock walls, boat channels, and changes to reef flat ecology can all result in changes to beach morphology and sediment budgets with erosion being the most common result.

### Future for reef cays

Cays are dynamic landforms that are mostly low and composed of unconsolidated sediments. They are widely perceived as particularly vulnerable to climate and sea-level changes projected as imminent consequences of anthropogenic activities (IPCC, 2007). Some believe that they are more resilient – that their dynamic nature will allow them to adjust. Some of the key potential impacts of sea level and climate changes on reef islands are schematically represented in Figure 9 and discussed further below.

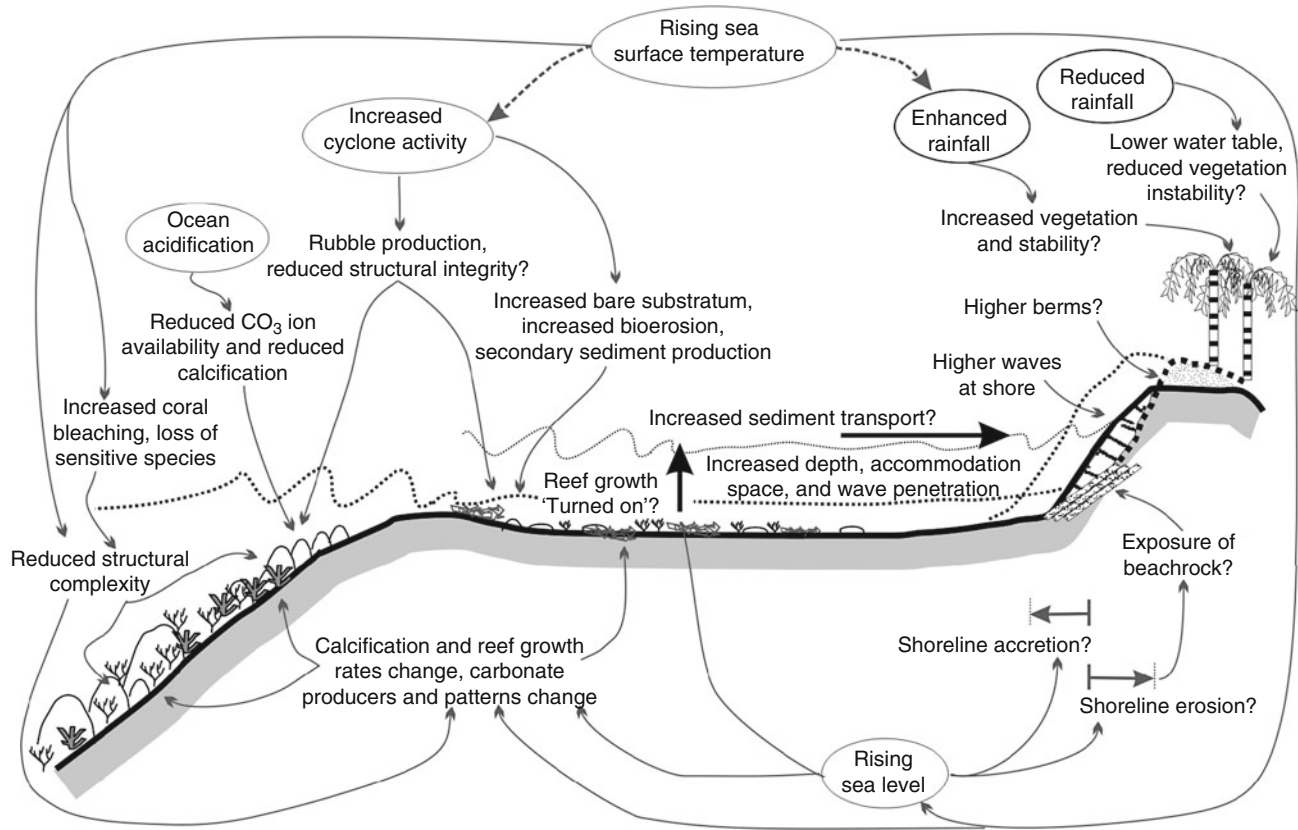
### Sea-level rise

Early concerns that sea-level rise will simply drown reef islands are now considered oversimplistic, with island response reflecting the complex interplay of numerous

physical, biological, and chemical factors. On some reefs, rising sea levels will allow larger waves to propagate further through more of each tidal cycle, increasing the transport of available sediment to islands. On reef flats affected by falling late Holocene sea levels, sediment deposits have accumulated and these may be mobilized shoreward – Hopley (1996) suggested that a sea-level rise of just 0.5 m would achieve this on many reefs. Hopley (1996) also modeled carbonate budgets for an idealized reef flat affected by a 0.5-m and 1.8-m rise by 2100 and showed that under the lower rate almost the entire reef would vertically accrete and reef morphology would not significantly change (see *Climate Change: Impact of Sea-Level Rise on Reef Flat Zonation and Productivity*). However, at the higher rate the algal zone transformed to coral cover, markedly increasing calcium carbonate production. The enhanced carbonate productivity would yield sediments suitable for reef-island construction, and because greater depth improves shoreward sediment transport, Hopley concluded that faster sea-level rise at first may be more beneficial for reef-island sustainability than a slower rate. Many reef geomorphologists agree that projected sea-level rise will substantially rework unconsolidated sediments and initially maintain reef-island mass (e.g., Kench and Cowell 2002).

The issue is more complicated, however, as elevation is critical on these low islands. Cay buildup is largely controlled by the characteristics of waves reaching the beach, with berm height – the height of the beach above mean high water – dependent on wave run-up. In a detailed study at Raine Island, Gourlay and Hacker (1991) found that the berm height was controlled by the wave run-up during the highest spring tides and calculated that the island may vertically accrete by an amount larger than the sea-level rise if reef flat aggradation lags behind the rate of sea-level rise and larger waves can reach the beach. However, given the diversity of reef-island morphologies, evolutionary histories, geographical settings, and human pressures, the future for reef islands may be diverse.

Late-Holocene emergence which has been demonstrated to be important to the formation and longer term stability of at least some cays has been discussed above. These factors would lose their influence as sea level increases. Uncertainties exist about future changes in storm frequency and intensity, but increases in both are possible. Higher wave energy might increase shoreline erosion, increase the frequency of inundation events, and threaten the quality and maintenance of groundwater aquifers and the long-term habitability of many reef islands. On Pacific Ocean, Indian Ocean, and Caribbean reef islands, settlements and vital infrastructure are almost without exception located close to the beach, where they are vulnerable to inundation, erosion, and other coastal hazards that may compromise the socioeconomic well-being of island communities. Understanding of some aspects of these interactions has advanced remarkably in recent decades. However, significant gaps still exist which limit capacity to confidently predict the long-term future



**Coral Cay Classification and Evolution, Figure 9** Schematic summary of potential climate and sea-level change impacts on reef islands.

of many reef islands. For example, simple models developed for linear and siliciclastic shorelines cannot be directly applied to reef islands.

### Reduced carbonate production and ocean acidification

There is heightened concern that thermal stress due to global warming (see *Climate Change: Impact on Coral Reef Coasts*) and changes in ocean pH associated with fossil fuel use (see *Ocean Acidification, Effects on Calcification*) is reducing both the amount of calcium carbonate produced on reefs and the durability of the sediments, both of which have the capacity to influence reef sediment budgets and ultimately the availability of sediments to maintain and build reef islands. The intensity and scale of coral bleaching has increased markedly since the 1960s, with entire reef systems affected by major events in 1998 and 2002 (see *Temperature Change: Bleaching*). Bleaching events not only affect corals, but also affect other photosymbiotic organisms such as foraminiferans that are very important contributors to many reef islands (Yamano et al., 2000). Calcification rates for corals on the world's best-managed reef – the GBR – are projected to decline by 14% compared to 1990 (D'earth et al., 2009) and it has been further

projected that coral cover will decline on reefs beyond 2050 (Hoegh-Guldberg et al., 2007).

Some reef islands accumulated most of their mass long ago, and these islands – especially if large and partially lithified – may be less sensitive to reduced carbonate production and ocean acidification in the short term. They will, however, be less able to dynamically adjust to projected changes in sea level and inundation. Where reef islands are younger, more mobile, and generally on less emergent reef flats, the future looks even less positive as active carbonate production and reef-island accumulation are more tightly coupled on lower reef flats, with efficient transfer of products to the zone of accumulation. In these circumstances, diminished carbonate productivity and sediment supply will probably have more immediate effects on island sediment budgets, morphologies, and prospects.

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## Cross-references

[Atoll Islands \(Motu\)](#)  
[Bassett Edges](#)  
[Beach Rock](#)  
[Cay Formation](#)  
[Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity](#)  
[Climate Change: Impact On Coral Reef Coasts](#)  
[Coral Cays, Vegetational Succession](#)  
[Engineering On Coral Reefs With Emphasis On Pacific Reefs](#)  
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[Steers, James Alfred \(1899–1987\)](#)  
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[Waves and Wave-Driven Currents](#)

## CORAL CAYS – GEOHYDROLOGY

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### Synonyms

Atoll island hydrology; Reef island geohydrology

### Definition

The geohydrology of coral cays relates to the movement of water through the island and reef framework under coral cays, particularly with respect to the characteristics of the freshwater resource resulting from density differences of freshwater and saltwater as affected by the composition and permeability of the reef framework in the context of its evolutionary history.

### Introduction

The earliest work on geohydrology applicable to coral cays was undertaken separately by Ghyben and Herzberg in the late 1800s and early 1900s, who determined the shape and thickness of a freshwater lens that forms under coral cays once they reach a minimum size. The relationship, which is based on the different densities of freshwater and saltwater, is expressed in the Ghyben–Herzberg equation:

$$z = \frac{\rho_f}{(\rho_s - \rho_f)} h,$$

where  $h$  is the distance above sea level to the water table (phreatic surface),  $z$  is the distance below sea level to the freshwater–saltwater interface, and  $\rho_s$  and  $\rho_f$  are the densities of saltwater and freshwater, respectively. Using densities of  $1.00 \text{ g cm}^{-3}$  for freshwater and  $1.025 \text{ g cm}^{-3}$  for saltwater gives the often quoted relationship

$$z = 40 h.$$

The Ghyben–Herzberg model makes an assumption of a single layer homogeneous medium, and a system in hydrostatic equilibrium, with no mixing of fresh and salt water, giving a sharp transition between the freshwater

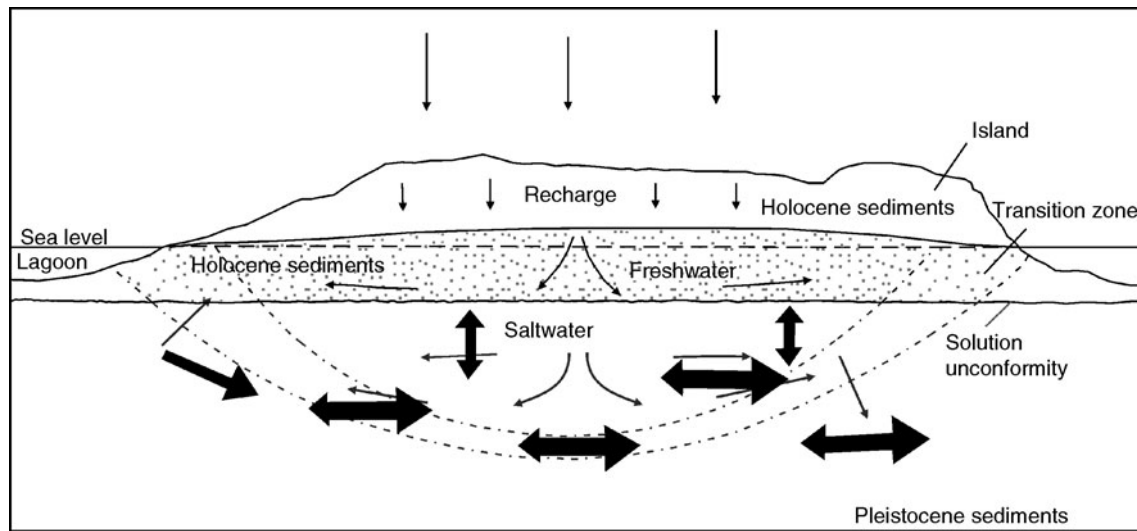
and saltwater. This model is normally implemented with the Dupuit assumption of horizontal flow (Oberdorfer et al., 1990) and is frequently applied in resource assessments of potable water for human use on inhabited coral cay islands.

In reality, this model makes assumptions that are clearly not valid in most coral reef environments. Tidal fluctuations of the water level are assumed to be negligible, water movement within the lens is assumed to result entirely from recharge-induced changes to the hydraulic head, outflow from the freshwater lens required to maintain mass-balance is assumed to take place at the island margin, and mixing within the framework caused by various water movements and pressure gradients (such as tidal mixing) is not considered. Perhaps most significantly, the assumption of a homogeneous medium rarely holds. In particular, differences in the reef framework above and below the Pleistocene solution unconformity (sometimes called the Thurber discontinuity) typically found 6–25 below the current reef flat level in tectonically stable areas, means that the model is fundamentally flawed. In general, a very broad transition zone between fresh and saltwater can be expected.

### The dual aquifer model

The framework below the Pleistocene unconformity is typically highly karstified with high porosity and permeability, due to exposure during much of the period since the last interglacial approximately 120,000 years ago (Vacher, 1997). Seawater can move effectively through the karstified framework, effectively truncating the freshwater lens at the unconformity (Figure 1). The hydraulic conductivity of the Holocene framework is probably 1 or 2 orders of magnitude less than that of the Pleistocene framework (Oberdorfer et al., 1990; Woodroffe and Falkland, 1997).

A two-layer (dual-aquifer) model with a moderately permeable Holocene reef framework overlying a high-permeability Pleistocene aquifer, proposed by Wheatcraft and Buddemeier (1981) has been developed and used by others in modeling and investigations of cay groundwater resources (Ayers and Vacher, 1986; Herman et al., 1986; Oberdorfer et al., 1990; Underwood et al., 1992; Griggs and Petersen, 1993; Bailey et al., 2009; and others). These studies have found a quantitative agreement between model results and physical and chemical field data, giving some confidence in the approach. Tidal flow through the Pleistocene framework has been shown to be particularly significant, overwhelming any density differentials that may limit mixing in the Pleistocene aquifer. Short-term vertical water movements of 1 m or less driven by horizontally directed (in the Pleistocene aquifer) and vertically directed (in the Holocene aquifer; Herman et al., 1986) tidal pulses control the nature of transition zone mixing (Underwood et al., 1992). Other short-term climatic events, such as storms, can also be reflected in water movements that cause mixing in the reef framework. Clearly, the use of the Ghyben–Herzberg–Dupuit model



**Coral Cays – Geohydrology, Figure 1** The Ghyben–Herzberg lens of freshwater truncated at the Pleistocene unconformity due to the highly karstified nature of the Pleistocene reef framework (Hopley et al., 2007).

leads to a significant overestimation of freshwater resources on almost all coral cays (Oberdorfer et al., 1990). Bailey et al. (2009) highlight the importance of cemented layers confining the freshwater in the Holocene aquifer. These occur at the reef flat surface, forcing freshwater to discharge in fractures in the cemented layer, or elsewhere on the reef. Hard layers at depth can direct flow, or otherwise confine flow.

### Lens thickness and freshwater resources

The thickness of the freshwater lens is typically in the order of 10–20 m on small coral islands (Falkland, 1993), although thinner lenses clearly exist on small islands, and thicknesses of up to 30 m have been measured. The shape of the lens may be asymmetric, typically deeper on the lagoon side of atoll islands (Falkland, 1993), probably due to the preferential accumulation of lower permeability sediments on the lagoon side (Anthony et al., 1989). Anthony (1997) notes that the position of the island on the reef flat, specifically with respect to the prevailing wind is an important determinant of the thickness of the freshwater lens, due to leeward reefs typically having finer subsurface deposits than those on the windward side of the reef platforms. The lower permeability deposits on the leeward island support thicker freshwater lenses than those on windward islands (Bailey et al., 2009). It is suggested by Bailey et al. (2009) that whereas the freshwater lens on leeward islands is truncated at the Pleistocene unconformity, the lens on the (typically smaller) windward islands may not extend to that level. From a number of examples drawn from the literature, windward island lens thickness is in the order of 2–11 m, compared to 12–20 m for leeward islands.

Numerical simulations using the dispersion (as opposed to sharp interface) model SUTRA (Voss and Provost,

2003) presented by Bailey et al. (2009), show clear relationships between recharge, hydraulic conductivity, depth to the Pleistocene unconformity and island width, and the thickness of the freshwater lens.

The lens thickness and consequent water availability (White et al., 2007) can be significantly affected by climatic events, particularly drought. Bailey et al. (2009) simulate El Niño conditions showing that a 6-month drought required a 1.5-year recovery period for the aquifer for islands in the western Pacific.

Modeling presented by Oberdorfer and Buddemeier (1988) show that the dual aquifer may have a significant influence on freshwater resources during times of climate change and rising sea levels. Counter-intuitively, because the depth of the freshwater layer is frequently truncated at the Pleistocene unconformity, a higher sea level may increase total freshwater resources, by opening up more lower permeability sediments for freshwater storage, as long as there is not a coincident loss of island area.

### Summary

The Ghyben–Herzberg model is generally inappropriate for the examination of the geohydrology of most coral cays due to the presence of high permeability reef framework below the highly karstified Pleistocene unconformity. A dual layer model, used by numerous authors has provided a good understanding of water flow and of freshwater resources under coral cays, with dominant horizontal saltwater flows through the Pleistocene framework truncating the freshwater lens, with tidally driven vertical movements through the lower-permeability Holocene framework, to which the freshwater lens is confined. The actual thickness of the freshwater lens is dependent on a number of variables, the most important of which is sediment permeability. Dual layer dispersion models are



being used to adequately describe water flow and the freshwater resource dynamics of coral cays.

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## Cross-references

[Atoll Islands \(Motu\)](#)  
[Cay Formation](#)  
[Holocene Reefs: Thickness and Characteristics](#)  
[Internal Circulation](#)  
[Last Glacial Lowstand and Shelf Exposure](#)  
[Solution Unconformities](#)

## CORAL CAYS, VEGETATIONAL SUCCESSION

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### Definition

Succession: A series of biotic communities replacing each other in an ordered temporal sequence, with each community creating conditions leading to the establishment of its successor.

Aeolian: Having to do with the wind.

Allochthonous: Coming from a source external to an ecosystem, community, or area.

Washover: The sea washing over an island during a storm.

### Early colonization

Continental islands have vegetation similar to that of and derived from the adjacent mainland. By contrast, cays have a much more limited subset of mainland floras, filtered by the vagaries of overwater dispersal; however, even for those, vegetation varies from sparse herbs, vines, and grasses to tall, dense forests. The present treatise deals with the causes of that variation and the temporal sequences through which cay vegetation pass.

The course of succession on cays depends on the type of substrate initially present. There are three main types associated with modern coral reefs. Sand cays begin as submerged sand bars that gradually accrete and eventually emerge from the sea. Rubble (or shingle) cays are formed suddenly by material from the reef being broken off and heaped onto the reef flat by a storm. In both cases, bare surfaces of sand or pieces of coral are exposed subaerially ([Figure 1](#)) and are available for colonization by terrestrial plants and animals, via some form of over-water dispersal. Mangrove cays differ in that plant succession begins before the cay itself forms. Propagules of mangroves are sea dispersed and take root in shallow water on reefs where they grow into trees. Dead leaves and other organic debris from these trees accumulate around the roots and eventually build up an organically rich mud that may in time become emergent above sea level. Some islands, of course, may be composites of more than one of these types.

Surprisingly, the first successful colonizers of bare cays may be animals, rather than plants. On the Great Barrier Reef of Australia, there are a number of sand cays, completely devoid of vegetation, that nevertheless have a fauna of up to 11 species of terrestrial invertebrates (Heatwole, 1971) such as flies, beetles, earwigs, mites, and isopods that subsist on dead marine organisms washed onto the beach, the carrion of marine intertidal invertebrates, and the excrement or cadavers of seabirds nesting on the island. On some cays, there are, in addition, predators such as centipedes and spiders, that feed on these terrestrial invertebrate scavengers. This assemblage thus depends either directly or indirectly on energy and



**Coral Cays, Vegetational Succession, Figure 1** Stages in the succession of vegetation on cays on the Great Barrier Reef of Australia. Top: bare sand cay; dark objects in the foreground are pumice (Bylund Cay, July 1988). Second from top: pioneer vegetation (Lady Elliott Island, 1969). Centre: cay with herb meadow (Bell Cay, July 1982). Second from bottom: savannah zone (Heron Island, January 1971). Bottom: Forest of *Pisonia grandis* (Northwest Island, July 1992). Photographs by Harold Heatwole.

nutrients from allochthonous marine sources, rather than from insular terrestrial ones. The organisms, such as sea-birds or crabs that connect the marine and terrestrial ecosystems and relay food from one to the other are known as “transfer” species.

The first plants to become established on bare cays are called “pioneer” species. They are usually transported there as seeds carried by sea currents. Many have special adaptations that improve their chances of dispersal in this way, such as devices that keep them afloat for long periods of time. In addition they need to be either impervious to seawater or resistant to high salinities. Not all species of seeds that are transported by water, however, are capable of becoming established on a bare island. Indeed, the beach wrack of many islands contains abundant seeds of species that have floated ashore but are not otherwise represented in the flora, either because the seeds did not survive the voyage, or because they were unable to germinate under the conditions they encountered upon arrival (Smith et al., 1990).

The successful pioneer species are those that combine the qualities of being able to withstand high salinities and salt spray, scarcity of water, shifting sands, low levels of nutrients in the soil, high temperatures, and bright sunlight. These are the conditions found on bare cays. The earliest pioneer vegetation consists of low herbs, grasses, and vines, often of a creeping habit (Figure 1). Species that put out runners over bare sand with roots descending at intervals are adapted to life on a shifting substrate as they tend to stabilize the sand. In time, pioneers may spread and cover much of the surface of a bare cay.

### Peripheral zone of shrubs

A few widespread, tropical shrubs, such as *Scaevola taccada* and *Suriana maritima* constitute a special category of pioneers. Perhaps the best example is Octopus Bush, *Argusia argentea*, a shrub/tree that is widely distributed throughout the Pacific and Indian Oceans. It has a buoyant corky layer around the seed that keeps it afloat for many weeks. It can survive for long periods at sea and in fact the seeds, although not germinating in seawater, germinate better after exposure to seawater. Seeds of this species are dispersed by sea currents over thousands of kilometers to be cast ashore on some remote island where, under the influence of rainwater, they germinate on the upper beach (Lesko and Walker, 1969).

These plants add a new zone of pioneer vegetation by forming a ring of shrubs that encircles the island (Heatwole, 1994). Octopus Bush is mainly on the upper beach as it seldom disperses even a few meters inland because seeds dropping from the parent tree have not been exposed to seawater (Figure 2). Where this shrub is found further inland it often is because the beach has extended since the plant became established. Once a shady, peripheral ring of shrubs has formed, it ameliorates conditions such that other sea-dispersed shrubs and trees find favorable germination sites.





**Coral Cays, Vegetational Succession, Figure 2** Zonation of vegetation on a cay on the Great Barrier Reef (Northwest Island, July 1992). There is a band of pioneer vegetation (*foreground*). The shrub "ring" is represented by a single young Octopus Bush (*Argusia argentea*) at high-tide line and a nearly continuous ring of older, tall Octopus bushes on an older level of the upper beach (*middle ground*; darker green), bordering the *Pisonia grandis* forest (*background*; lighter green). Note the recent erosion of the upper beach. Photograph by Harold Heatwole.

### Herb meadows

Pioneer species stabilize shifting sand, shade the surface of the ground, and through adding dead leaves and other organic matter enrich the soil (Wiens, 1962) and begin to form a soil profile. In addition, the shrub ring serves as a windbreak, provides more extensive shade, and screens out salt spray. Providing sufficient fresh water becomes available, these changes facilitate inland conditions that are favorable for species that could not colonize a beach or a bare cay. Very small sand cays have little permanent fresh water but as they grow larger through further accumulation of sand, they surpass the critical size for retaining

rain as a lens of freshwater in the soil (Wiens, 1962). The stage is now set for the establishment of species of non-pioneer plants. Most of these new colonists are dispersed by birds, either attaching by hooks or sticky secretions to feathers of a variety of birds, including seabirds, or are carried in the digestive tracts of seed-eating or fruit-eating birds. Once deposited in their new home, they grow and form a meadow of herbs and grasses (Heatwole et al., 1981) (Figure 1). The pioneers either find the new conditions unfavorable to them, or are out competed by the new arrivals and they decline, leaving the center of the island covered by the second wave of colonists. The cay is now zoned, with pioneer species still dominating the upper beach, followed behind by a shrub ring and with a central meadow of herbs and grasses.

### Savannah

With increasing bird traffic attracted to the greater plant cover in the interior, the number of species of plants there builds up, including a variety of trees and shrubs that shade the island's central habitat still further and contribute greater amounts of organic matter to the soil. In this way the herb meadow becomes dotted by scattered shrubs and trees to form a savannah (Figure 1), sometimes called parkland. Trees that are common in the savannahs on cays are *Cordia subcordata*, *Calophyllum inophyllum*, *Hernandia peltata*, and *Guettarda speciosa*. Humans have often contributed to this zone by plantations of coconuts (*Cocos nucifera*).

### Forests

Over time, the density of arborescent vegetation increases until a forest forms, complete with a ground cover of leaf litter and a more mature soil profile. Species of sea birds, such as the Black Noddy (*Anous minutus*) that require trees for nesting, roost in large numbers in these forests and contribute massive amounts of guano to the soil. Most species of low vegetation of the herb meadow or savannah cannot tolerate the dense shade and high nitrogen levels under the forest and accordingly they disappear, leaving only a sparse cover of nitrophilous plants. Now, the zonation includes a peripheral ring of pioneer species surrounding a shrub ring, with the interior of the island covered by forest or a combination of forest and savannah. All of these stages in the succession of vegetation can be seen on islands on reefs (Figure 2). The forested islands seem to be the end stage in this sequence as no further stages have been witnessed. This does not mean that change ceases, however, or that all islands inevitably reach this final stage. Because of that, some ecologists dispute the validity of the concept of succession. Further changes, however, can be viewed as intervention by forces or agents that halt or reverse what would otherwise be an orderly progression. Some of these retrograde, destructive influences are known (Heatwole, 1984) and are as follow:





**Coral Cays, Vegetational Succession, Figure 3** Gannet Cay, Great Barrier Reef (January 1989), a cay that was once much larger and with a well developed herb meadow. It was formerly located farther onto the reef, toward the top of the picture. The automatic weather station seen in the center of the picture was once located in the center of the island. The island has now shifted to the edge of the reef and is losing sand to deeper water as seen by the cascade of sand toward the left end of the island. Photograph by Harold Heatwole.

### Erosion

The pattern of zonation of vegetation, described above, can be obliterated by erosion. As direction of prevailing winds shift, or local patterns of sea currents change, beaches on one side of an island may erode and encroach into a herb meadow or even a forest. Often, the beach on the opposite side of an eroding island is prograding and widening the zone available for pioneer vegetation. Thus, instead of concentric vegetation zones, they are off center and lopsided. In extreme cases, cays can move across the reef, eroding on one side and prograding on the other, until eventually, the position of the cay scarcely overlaps that of its former location (Flood and Heatwole, 1986), or a cay may go over the edge of its reef into deep water and disappear altogether (Figure 3).

### Marine washover

Severe storms may result in a cay being washed over by waves and the terrestrial vegetation destroyed (Flood and Heatwole, 1986), with succession having to start over again. The history of some islands can be seen in heavily eroded beaches where dark layers of humus (indicating previous times of vegetation cover) are interleaved with layers of light-colored sand (left from times when the island was devoid of vegetation, either because of marine washover or from Aeolian deposition of sand on top of the plants) (Figure 4).

### Seabirds

The role of seabirds as transfer organisms, as dispersers of seeds, and as enrichers of the soil, has already been discussed. Birds may also have a destructive effect. Where



**Coral Cays, Vegetational Succession, Figure 4** A highly eroded beach on Frigate Cay (July 1987) showing alternating layers of dark organic humus and lighter-colored sand, representing successive periods of vegetation cover and bare sand at the surface. Note that encroachment on the herb meadow by erosion has exposed roots of *Boerhavia diffusa* (upper left).

they nest on a herb meadow in large numbers, their trampling may destroy plants (Heatwole, 1984) and return the island to a previous stage, or even to a bare cay. This is especially likely to occur if the breeding colony is being concentrated into smaller space by continued erosion of an island on one edge of its reef, while the prograding side goes over the edge into deep water.

### Sea turtles

When sea turtles come ashore to nest, the female digs a pit in which she lays her eggs; in the process she may kill plants by uprooting them (Figure 5). Species of the herb meadow are more susceptible because they usually occur as individually rooted plants. By contrast, many pioneer species have runners with multiple root systems, so that even if a large part of the plant is dug up other parts of it



**Coral Cays, Vegetational Succession, Figure 5** Nesting sea turtles dig pits in the sand in which they lay their eggs. This activity leaves an uneven terrain of hummocks and pits, as seen in this photograph. The uprooted vegetation dies (*foreground*). Such destruction by turtles can lead to return of herb meadow (without creeping plants) to pioneer vegetation that is anchored over a wide area by runners. Photograph by Harold Heatwole.

still have roots in the soil and the plant can survive. For this reason, where turtles nest in high numbers, succession may be halted or herb meadow even reversed to pioneer vegetation (Heatwole, 1984; Rogers 1989).

### Drought

Even in such an equable environment as a tropical island, the weather is not constant. There are year-to-year changes in the amount of rainfall, and these can affect the trajectory of vegetational succession on cays. There has been only one detailed study of this phenomenon and that was on One Tree Island at the southern end of Australia's Great Barrier Reef from 1968 to 1978 (Heatwole, 1981; Heatwole et al., 1981). Rainfall was plentiful for most of the time, but there was a drought of four months, that

killed a lot of vegetation. No species of plant went extinct because of the drought, but the most abundant species of the herb meadow (*Melanthera biflora*) declined to less than a quarter of its former biomass. By contrast, a pioneer species (*Ipomoea pes-caprae*) that had been rare in the herb meadow before the drought thrived and increased greatly in biomass to become the dominant species. Thus, the drought caused vegetation in the center of the island to revert to a previous successional stage.

### Humans

Humans have a major effect on cays, through direct destruction of vegetation and fauna, construction of buildings, mining guano, altering patterns of erosion, planting gardens and coconut groves, and introduction, intentional or otherwise, of weeds. Lady Elliott Island on the Great Barrier Reef is an example of both good and bad effects of humans. It was first nearly denuded by guano miners who destroyed the vegetation and stripped the soil. Later, it was restored to nearly its former condition by replanting native vegetation as part of the development of an eco-friendly resort.

### Summary

As a bare cay forms and increases in size, its vegetation goes through a predictable progression of successional stages: bare cay → pioneer vegetation → pioneer vegetation plus encirclement by shrubs → herb meadow → savannah (parkland) → forest. Plants of the earliest stages tend to be sea-dispersed whereas later the vegetation consists mostly of bird-dispersed species. The vegetation becomes progressively organized into concentric zones with earlier successional stages located peripherally and later ones successively toward the center. This sequence can be altered, or reversed, by various destructive forces, including trampling by seabirds, uprooting of vegetation by sea turtles, drought, erosion of beaches, washover during storms, and human activities.

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## Cross-references

[Coral Cay Classification and Evolution](#)  
[Cay Formation](#)  
[Unvegetated Cays](#)  
[Vegetated Cays](#)

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## CORAL REEF, DEFINITION

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### Definition

*Coral reef*: A tract of corals growing on a massive, wave-resistant structure and associated sediments, substantially built by skeletons of successive generations of corals and other calcareous reef-biota.

*Coral-algal reef*: A rigid wave-resistant structure in which scleractinian (stony) corals and crustose coralline algae are the dominant frame-builders. The term “modern” is used to refer to reefs that are forming or have formed in response to late Holocene sea levels (less than 7000 years B.P.) (James and Macintyre 1985).

### Introduction

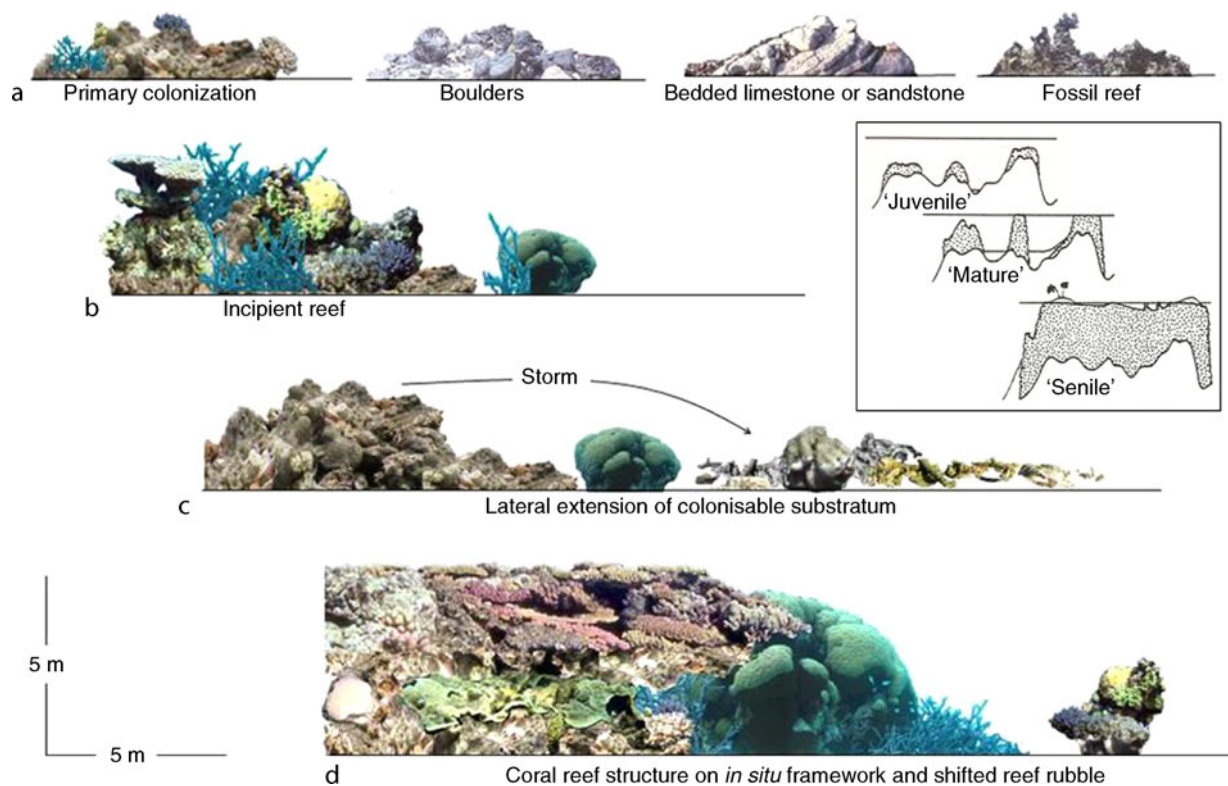
Drawing a parallel with a definition of the coral reef's nearest terrestrial equivalent “forest” as “large tract covered with trees and undergrowth” (Fowler, 1929), “coral reef” could simply be defined as “large tract covered with corals and undergrowth.” However, these words fall well short of capturing a coral reef's total character on two major fronts (Stoddart, 1969): first, the notion that the organisms of the reef themselves do not simply cover a tract, but also contribute to its nonliving physical structure (Figure 1) in a way that has no parallel in forests; second, the rich and complex ecological systems of which the corals are part. Documentation of variation in form and process started with Darwin's (1842) recognition of oceanic fringing reefs, barrier reefs, and atolls as a developmental series on subsiding volcanic islands. Such reefs, whose surrounding water depths and thickness

exceed 1,000 m, represent the outcome of episodes of reef growth, punctuated by sea-level change, since the Tertiary (Hopley et al., 2007). Other impressive coral reefs are much thinner and much younger, exemplified by reefs on the shallowest parts of continental shelves that were >100 m above sea level as recently as 20,000 y BP and became inundated as recently as 7,000 y BP. There, water depths and reef thickness can be less than a few meters, the entire entity representing reef initiation and growth of the mid to late Holocene epoch (Kennedy and Woodroffe, 2002).

A terminology for coral reefs based on their relationship to land mass and depth of surrounding water (Figure 2c; see also James and Macintyre, 1985; Spalding et al., 2001) includes the following: “fringing reef” (a linear reef with a reef flat some tens of meters across, growing along shelving coastlines and across embayments); “bank barrier reef” (another form of linear coastal reef a little further from the shore than the fringing reef, and sometimes coalescing with one); “barrier reef” (also a linear structure, but fronting deep oceanic waters and broader – usually hundreds of meters across – and separated from the coastline by navigable waters); “atoll” (broadly circular reefs enclosing a wide lagoon); “bank reef” or “platform reef” (a substantial reef fitting none of the above categories, occurring in oceanic and coastal settings). Collectively, these terms account for most of the large scale morphological variability observed in tropical coral reefs. Coral reefs that are substantially built by skeletons of successive generations of corals and other calcareous reef-biota also exist in deep, cold waters (Roberts et al., 2006). However, these “cold-water coral reefs,” located at depths well below the impact of breaking waves, are not “wave-resistant” structures in the same sense as shallow tropical reefs.

Smaller scale morphological variability within and among reefs is very strongly determined by the “antecedent topography” on which corals established themselves (Shinn et al., 1977) – i.e., the location, shape and time of Holocene inundation of topographic sea-floor high points of stable substrata (e.g., rocks, fluvial rubble, fossil carbonate reefs or dunes). From the mid-Holocene to the present, primary colonization and the upward and outward accumulation of calcium-carbonate skeletons across that topography has adorned and obscured its shape to varying degrees. This transformation has been represented in whole reefs as a progression through a development series from “initiation” through “juvenile,” “mature,” and “senile” stages (Figure 1; see also entry *Reef Classification by Hopley (1982)*), a scaled-up manifestation of the series of local scale transitions “a” to “d” in Figure 1 and Figure 2a. In “resorbed” and “remnant” reef structures (see entry *Reef Classification by Maxwell (1968)*), “degenerative” processes have prevailed, as cumulative loss of reef material through storms and erosion (both biological and physical) exceeds accumulation of reef material; the net transitions have been in the reverse direction (e.g., “d” to “c,” “b” or “a”)

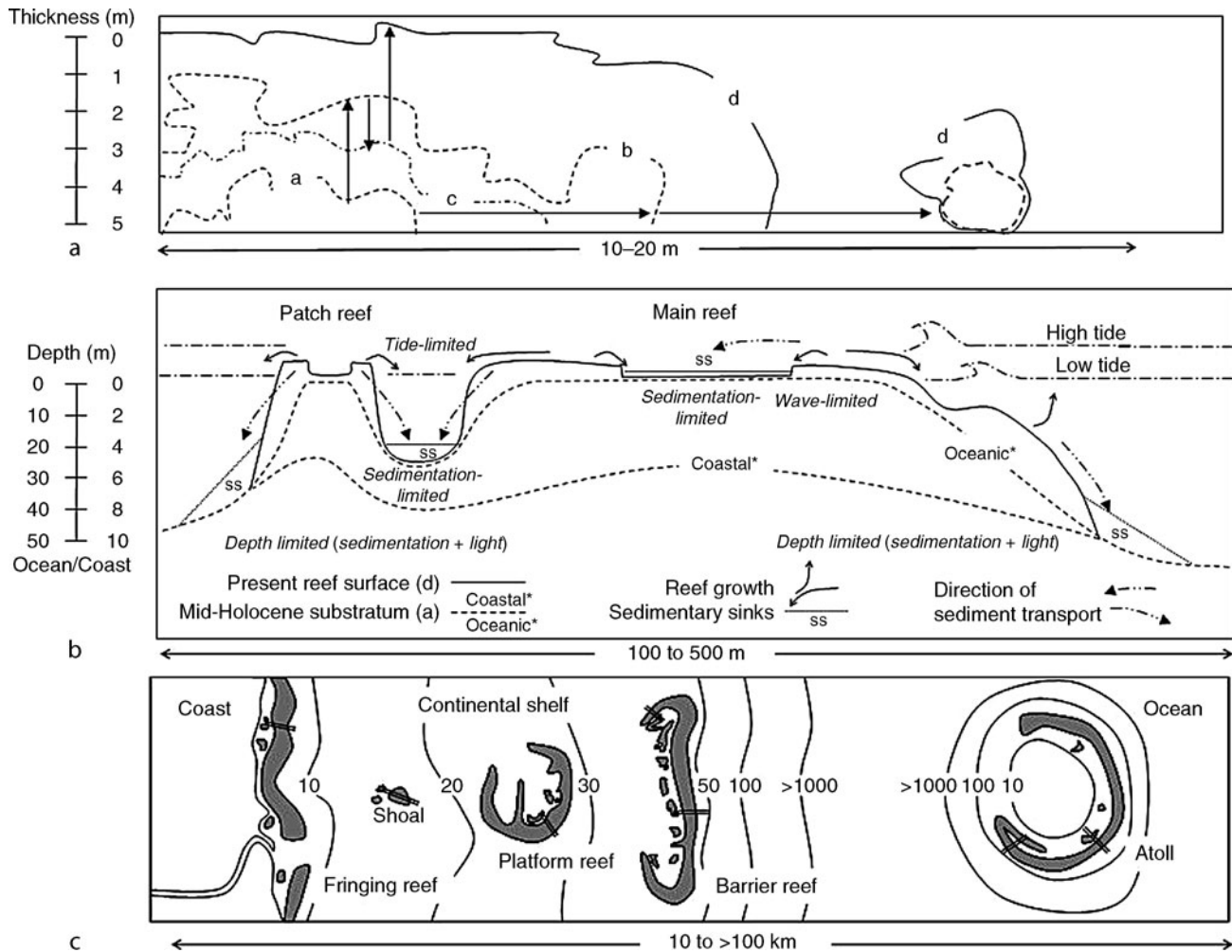




**Coral Reef, Definition, Figure 1** Reef growth model. Inset: Hopley's classification of shallow reefs according to their stage of Holocene development (shown as stipple; see also entry *Reef classification* – Hopley 1982). Main section: Local scale processes and events responsible for reef growth. (a) Primary coral colonization of newly available substratum and examples of types of substrata made available by last sea-level transgression: boulders (e.g., fluvial; littoral); bedded limestone or sandstone; fossil reef (pitted by subaerial erosion). (b) Incipient reef. Coral–algal framework with or without sediment infilling has developed over the substratum in (a). (c) All the corals and part of the framework have been torn off by storm waves and scattered on the adjacent sea floor, extending the colonisable substratum. One large massive coral remains intact and in place, and another has been thrown clear of the developing reef. (d) The surface of the incipient reef has been recolonized and further framework added, filling the space between the developing reef and the first massive coral, now much larger. The massive coral tossed off the reef in (c) died and has become substratum for more coral growth. It may in time be moved by another storm, and/or become incorporated into the developing reef. In shallow water, further upward growth of corals and hence the structure will eventually be limited by exposure to the air. In deeper water, further upward growth may occur, or it may be limited by destructive waves (see entry *Corals – Environmental controls on growth*).

The James and Macintyre definition of “coral–algal reef” (above) gives coralline algae equal prominence with stony corals, recognizing their role both in accreting thick algal ridges and in cementing coral skeletons together into a framework. Their definition works extremely well for oceanic reefs worldwide, in which the necessary resistance to powerful ocean waves is inconceivable without the major contribution made by coralline algae. However, the term “coral reef” is also used to describe coral tracts sitting atop accumulations of coral debris with little or no submarine cementation: e.g., cold water reefs (Roberts et al., 2006) and many tropical fringing reefs, shoals, mounds, and banks. This raises the question of whether these latter forms should be excluded and called something else, or included under a more generic definition such as the first one presented above. It would be difficult to apply the James and Macintyre definition – with its

emphasis on cementation by coralline algae – to many of the mega-diverse coral reefs in sheltered waters of South-East Asia (Spalding et al., 2001; see *East Indies Triangle of Biodiversity*), the Great Barrier Reef lagoon (Johnson and Risk, 1987; Hopley et al., 2007; Perry et al., 2008), or the rhomboid shoals behind the Belize Barrier Reef. The latter have been described in terms that could be used to describe reefs in sheltered waters in many parts of the world: little submarine cementation; corals stabilized by interlocking of their skeletons; colonies growing to the point of oversteepening and toppling down slope; debris fans at their base; only occasional storm disturbance (Aronson and Ellner, 2007). Lacking major cementation, and lacking exposure to the ocean's strongest waves, their wave-resistance is less in absolute terms than that of oceanic coral–algal reefs. They have, nevertheless, like “coral–algal” reefs, elaborated in the mid- to



**Coral Reef, Definition, Figure 2** Coral reef structure at scales of metres to 100s of kilometers. (a) Position of reef surface at stages “a” to “d” in Figure 1. Vertical arrows show accumulation (up arrows) and interruption of vertical growth by the storm in Figure 1c (down arrow). Horizontal arrows show the extent of lateral spread of colonisable substrata, providing the potential for the reef to “step out over its own debris” (Blanchon and Jones, 1997). (b) Profile of generalized coral reef exposed to waves from the right. The present reef surface has developed over the mid-Holocene substratum (dashed lines) by processes illustrated in Figure 1. (\* Note the five times difference between the vertical scales for coastal and oceanic reefs). The major growth directions, sediment movement and dominant environmental factors limiting coral growth and framework development are indicated: viz. light, sedimentation (rate of sediment fall), waves, tide (= exposure to air). (c) Diagram of some major reef types and bathymetric settings of coral reefs. Double lines indicate positions of cross-reef transects that could be represented by Fig. 2b. Contours indicate depths in meters. Continental shelf extends from coast to 100 m isobath.

late Holocene as structures widely referred to among scientists as “coral reefs.” Their smaller dependence on algal cementation and strong framework is evident in a number of modes of growth in fringing coral reefs (Kennedy and Woodroffe, 2002), in which lateral reef growth over unconsolidated coral debris is prominent. In summary, the first definition (see section ‘Definition’) is preferred here because it accommodates both the “classic” coral-algal reef style defined by James and Macintyre (1985) and also coral tracts established on less strongly consolidated substrata.

### Coral community: geological and ecological definitions

Further differentiation is provided by Buddemeier and Hopley (1988), who distinguish between “coral reef,” “coral reef community,” and “coral community.” They use “coral reef community” to refer to an incipient coral reef (Figure 1b) – not yet a massive wave-resistant structure, but on a developmental trajectory toward that state. Their “coral community” is on no such trajectory: it refers to a local assemblage of corals that are attached directly to nonreef substrata and provide no indication that their

predecessors have, or they and their successors will, substantially expand the substratum the way incipient reefs do. The state illustrated in [Figure 1a](#), assuming it was representative of an area of at least hundreds of meters, would be referred to as “just a coral community” so long the corals failed to add to a wave-resistant framework, either in situ or by ending up in a congruent rubble bank.

These terms are useful in placing “coral reef” on a “not-reef” to “reef” continuum, defined in terms of realized or potential “structure.” However ecologists use these terms differently: “community ecology” is a rich and long established discipline that focuses on environmental and biological drivers of “structure” in plant and animal communities (May, 1985). “Structure” in a community refers not to physical form, but rather to spatial pattern, species composition, population dynamics and the like. As a simple descriptive term within reef ecology, “a coral community” refers to the corals occupying a local area, irrespective of its substratum (e.g., Done, 1982), and a “coral reef community” refers to the entire ensemble of marine species that occupy a coral reef, and among which the “coral community” is a part. Coral reef communities are extraordinarily rich in species and co-evolved relationships, with important functional roles that facilitate tight recycling of nutrients in nutrient-poor waters (Hallock, 2001), survival in turbid seas (Perry et al., 2008a), and high per unit area productivity of protein, reef building blocks and sediments (Done et al., 1996). The terms “coral community” and “coral reef community” thus have contrasting nuances for earth scientists and biologists. However, their meaning will usually be clear according to the context in which they are used.

The measure of a good definition is the extent to which it eliminates similar entities. In the following sections, the definition is dissected and the terms elaborated using both examples and exceptions. [Table 1](#) describes some of the relevant terms.

### A tract of corals

Tracts (viz. “large areas of indefinite extent”) of living corals provide food and shelter for much of the abundance and diversity of marine biota for which coral reefs are renowned. In two circumstances, however, living corals are absent – or they are at least too sparse to be reasonably referred to as a “tract” – from what would still be considered legitimate contemporary coral reefs: “dead” and “marginal” coral reefs. In “dead” coral reefs, absence or scarcity of corals is a consequence of a recent (within a human life span) catastrophic impact (e.g., predation, disease, coral bleaching, cyclone). Regardless of whether the corals recover expeditiously (years to decades), this structure would still be considered a “coral reef,” albeit “dead,” or in an alternate or phase shifted state (Done, 1992; McClanahan et al., 2002). In “marginal” coral reefs, corals are sparse or absent from reef substrata because the supply of coral larvae or viable fragments no longer exists, and/or on-site environmental conditions have become inimical for corals. There are, for example, “drowned reefs” that supported flourishing coral communities before the sea-level transgression but where light is now limiting and sedimentation is excessive for good coral growth and survival. And there are back-reef areas for which the reef’s own growth has so greatly changed water circulation that

**Coral Reef, Definition, Table 1** Brief glossary of useful terms for describing generic characteristics of corals and coral reefs at spatial scales from <1 mm to hundreds of kilometers. An example of specific reef types is provided in [Figure 2c](#)

| Term/alternative                                              | Description                                                                                                                                                                                                                                                                                                                                                      |
|---------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Larva/planula larva                                           | Free living soft-bodied embryo that settles on a solid substratum and forms a primary polyp                                                                                                                                                                                                                                                                      |
| Primary polyp                                                 | The polyp into which the larva metamorphoses                                                                                                                                                                                                                                                                                                                     |
| Zooid                                                         | A polyp and its corallite                                                                                                                                                                                                                                                                                                                                        |
| Corallite                                                     | The limestone cup that is secreted by each polyp and provides it with structural support                                                                                                                                                                                                                                                                         |
| Corallum                                                      | The limestone skeleton of a coral colony                                                                                                                                                                                                                                                                                                                         |
| Colony                                                        | The limestone skeleton plus the living polyp tissue, produced by replication of the primary zooid and all its descendants.                                                                                                                                                                                                                                       |
| Population                                                    | All members of one species living in a defined area, such as a single coral reef. In a regional context, the single reef’s population is a “sub-population” of a regional “metapopulation.”                                                                                                                                                                      |
| Community/assemblage                                          | All colonies of all species occupying a defined area, such as a reef or a specific part of a reef                                                                                                                                                                                                                                                                |
| “Bommie” (Australian vernacular, widely used internationally) | 1. A “head” coral two to several meters high and across                                                                                                                                                                                                                                                                                                          |
| Patch reef                                                    | 2. A patch reef<br>A number of corals of one to many species growing on a discrete patch of reef substratum associated with a larger structure referred to as the “main reef” in <a href="#">Figure 2b</a>                                                                                                                                                       |
| Coral reef/coral reef complex                                 | See “Definition” (above) and “ <i>Coral Reef – classification</i> .” Its basal footprint (delimited by consolidated reef and adjacent sedimentary deposits) is usually measured in hectares or square kilometers. A coral reef always includes a discrete main section and often includes bommies and patch reefs in the footprint ( <a href="#">Figure 2c</a> ) |
| Reef tract                                                    | All contiguous and adjacent coral reefs within a particular region. Depending on commonality of the environment and the strength or weakness of material exchanges among them, the reefs in a tract may be considered to constitute a “system,” in which the state of one may influence the state of another                                                     |



regimes of temperature, oxygenation, salinity, and turbidity have become inimical for coral growth (Macintyre, 2007).

### Massive structure

A coral reef is “massive” (relative to the size of a human observer) in terms of both its basal area (usually hectares and upward) and its thickness (a nonliving basement usually meters to tens of meters thick and the living corals and diverse other sessile biota attached to it – usually <1 m to a few meters tall). Coral covered substrata of smaller dimensions than these could still legitimately be referred to as “coral reefs,” but so long as they were in close vicinity to a larger structure, they would generally be referred to as “patch reefs,” and considered to be a physically discrete part of the larger unit: e.g., the patch reefs at the back of such and such a reef.

A generalized picture of the “classic” reef-building processes based on James and Macintyre (1985) and Kan et al. (1997) is as follows: large corals of diverse and irregular shapes remain in place after their death, forming roofed-over cavities (robust branching forms such as *Acropora palmata* – James and Macintyre, 1985) or stacks of head and branching corals (Kan et al., 1997) – the whole becoming a “framework” that becomes inhabited by smaller attached calcareous benthos. Encrusting organisms (calcareous algae) grow over dead surfaces, aid in stabilizing the structure, and provide environmental cues that promote settlement of new corals (Harrington et al., 2004). Assuming there is sufficient water above (Figure 1; see entry *Accommodation Space*), another layer of corals can thereby settle, grow, die, become incorporated into the reef framework, and thus incrementally thicken the reef structure (Pichon, 1974; Kan et al., 1997). In stormy weather (Figure 1c), weakly attached or branching corals are broken, dislodged, and deposited in reef cavities and skeletal conglomerations on the reef slope or adjacent sea floor, allowing the reef to extend laterally by “stepping out over its own debris” (Blanchon and Jones, 1997). The latter process may be a result of settlement of coral larvae on the debris, or regeneration of still viable coral fragments among the rubble.

Another equally important process is infilling. The developing framework can be buried by or partially filled with sediment, with grain sizes from fine silts to coarse rubble, either before or after significant cementation has taken place. The types of corals, types of sediments, stage of cementation, and time and rate of burial produce distinctive layers in the sedimentary profiles of the reef (Shinn et al., 1977) that are reflected in distinctive limestone rocks in fossilized reefs (James and Macintyre, 1985; e.g., see entries *Rudstone*, *Bafflestone*, *Framestone*, *Floatstone*).

### Wave resistant structure

All coral reef definitions specify a structure that is highly resistant to wave impacts. Strong swells and waves do sometimes damage framework and cause catastrophic losses to reef biota (see entry *Tropical*

*Cyclone/Hurricane*). However, the change (in terms of tonnes of reef debris created and moved) is generally insignificant compared to mass and volume of reef framework that remain intact and in place. Moreover, the dissipation of wave energy across reef flats, the refraction of waves around reefs, and the flushing of sand through canyons by return flows are highly instrumental in determining the shape of reefs (Blanchon and Jones, 1997). Such a wave on reef interaction promotes the retention of reef-derived blocks, rubble, and finer sediments within the existing reef footprint, and thus the reef’s propensity to “step out.”

### Associated sediments

Coral reefs generate massive amounts of carbonate sediments. Fine sediments (sands and silts) are derived from both bioerosion of large metazoans such as corals, and the post-mortem disintegration of other calcifiers, notably foraminifera, small molluscs, and diverse segmented calcareous organisms including coralline algae and crinoids (James and Macintyre, 1985). Coarse sediments (boulders, blocks, rubble, shingle) are moved by storms, currents and gravity (see above and entries *Tropical Cyclone/Hurricane*, *Hydrodynamics of Coral Reef Systems*). They fall into lower energy deposition sites, including crevices within the reef, talus beds at the base of reef slopes, reef-flat boulder ramparts, sheltered back-reef lagoons and aprons, and gutters. In reefs far from land, most if not all sediments are generated by the reef. However, on some coastal reefs, sediments of terrestrial origin can dominate infilling sediments and the near-reef sedimentary apron (Kleypas et al., 2001; Larcombe and Carter, 2004). These imported sediments may include (1) sediments from the present-day land mass (via surface runoff, dust or ash) and/or (2) sediments from now-submerged mid-Holocene coastal low lands, re-suspended and swept into and around reefs by currents and waves (Larcombe and Carter, 2004).

### Substantially built by successive generations of corals and other reef builders

Over scales of decades to millennia, reef growth is dependent on ecological resilience in the resident stony coral populations and other reef builders – their capacity to recover dense populations following those necessary physical disturbances that transform some of them into debris. In a well functioning reef, “other reef builders” perform a number of direct and indirect “bioconstructional roles” in addition to the primary framework building role of stony corals and encrusting coralline algae (Done et al., 1996): “secondary framework builders” such as byozoans and bivalve molluscs and tube worms add small scale topographic complexity to the framework; microbes condition substrata for coral settlement and contribute to wave-resistance through submarine lithification; “non-framework reef builders” such as foraminifera, erect coralline algae (especially the genus *Halimeda*) and molluscs contribute greatly to reef sediments; “sediment

operators,” such as holothurians and burrowing worms and molluscs, aerate sediments and contribute to the productivity of sandy lagoons; “facilitators” such as herbivorous fishes and invertebrates keep algal biomass in check that might otherwise limit coral settlement and survival.

Resilience in biota and functional roles is as much dependent on the existence of the wave-resistant structure as it is a contributor to it. A critical third pre-requisite is a hydrodynamic setting that acts to retain the reef debris within the existing reef footprint. Reefs with this combination of resilient populations of corals, other reef builders and facilitators, high carbonate production, and strong retention have been termed “production-dominated” (Kleypas et al., 2001). These authors note that a reef’s potential for this strongly autonomous growth may be limited in three ways: by a location and hydrodynamic setting that favors import and incorporation of exogenous sediments – marine or terrigenous (“import-dominated” reefs); export of reef-generated sediments (“export-dominated”); or such a poor larval supply and/or conditions for coral growth that it cannot keep up with losses caused by bioerosion (“bioerosion dominated”). This latter style is classically represented in back reef areas that become isolated from the ocean by the coral reef’s own profligate growth (Macintyre, 2007).

“Coral communities” (*sensu* Buddemeier and Hopley, 1988; i.e., those that do not advance beyond stage “a” in Figure 1) are extreme examples of an “export-dominated” setting. These corals settle directly on “non-reefal” substratum, and on their death, are physically and biologically eroded down to silt, or fall off (precluding framework accretion and sedimentary infilling), and are carried by currents and gravity into places too deep, too turbulent or too sandy for additional coral settlement or survival.

“Incipient reefs” (a term preferable to “coral reef communities”; Figure 2b) are coral reefs in the making. They have had insufficient time to complete sufficient incremental vertical growth and “stepping out” to be considered a “coral reef.”

## Summary

Two similar definitions (“coral reef” and coral-algal reef) are provided, one strictly geological and one that specifies *living* corals as a fundamental defining characteristic of “coral reef.” The definition is then dissected, and allied terms such as “coral community” and “coral reef community” discussed, noting the completely different meaning of these terms in geology and ecology. The importance of ecological processes in keeping up the supply of building blocks (corals and reef debris) is discussed. Differences in local environment and in particular, hydrodynamic setting, lead to different intergenerational performance of coral populations, and also the propensity for reefs to act as sediment importers, producers or exporters, or to be in a state of net loss due to bio-erosion. A place’s environmental regime considered over decadal time scales and up (including “normal” conditions and extreme

events) will determine the likelihood of a coral community making the transition (Figure 1) to an “incipient coral reef” (early stages of development of a wave resistant structure) and a “coral reef” proper. Key determinants are first, whether there is a sufficient density of corals in a sufficiently large area that grow long enough and get large enough to create a wave-resistant structure; and second, whether that structure gets large enough to attenuate and refract waves and currents in a manner that promotes the retention and compaction of its own biogenic sediments within and around itself.

Just as the terms “juvenile,” “mature,” and “senescent” are applied to the coral reefs as geological structures, so are they applied to the tracts of corals for which the structure is simply “substratum.” However, the links between coral dynamics and reef development are poorly understood (Perry et al., 2008b). Improved understanding is important, especially in light of serious, persistent, and widespread declines in coral cover and resilience (e.g., Bellwood et al., 2004) and some very bleak projections for the future of coral reefs under global climate change (Veron, 2008).

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## Cross-references

Accommodation Space  
 Bafflestone  
 Barrier Reef (Ribbon Reef)  
 Climate Change and Coral Reefs  
 Corals: Environmental Controls on Growth  
 Cold-Water Coral Reefs  
 Darwin, Charles (1809–1882)  
 East Indies Triangle of Biodiversity  
 Ecomorphology  
 Eco-Morphodynamics  
 Floatstone

Framestone  
 Fringing Reefs  
 Geomorphic Zonation  
 Hydrodynamics of Coral Reef Systems  
 Mid Holocene  
 Patch Reefs: Lidar Morphometric Analysis  
 Reef Classification by Fairbridge (1950)  
 Reef Classification by Hopley (1982)  
 Reef Classification by Maxwell (1968)  
 Reef Flats  
 Reef Typology  
 Reticulated Reefs  
 Rudstone  
 Sedimentation Stress  
 Tropical Cyclone/Hurricane  
 Turbid-Zone and Terrigenous Sediment-Influenced Reefs

## CORAL REEFS OF INDIA

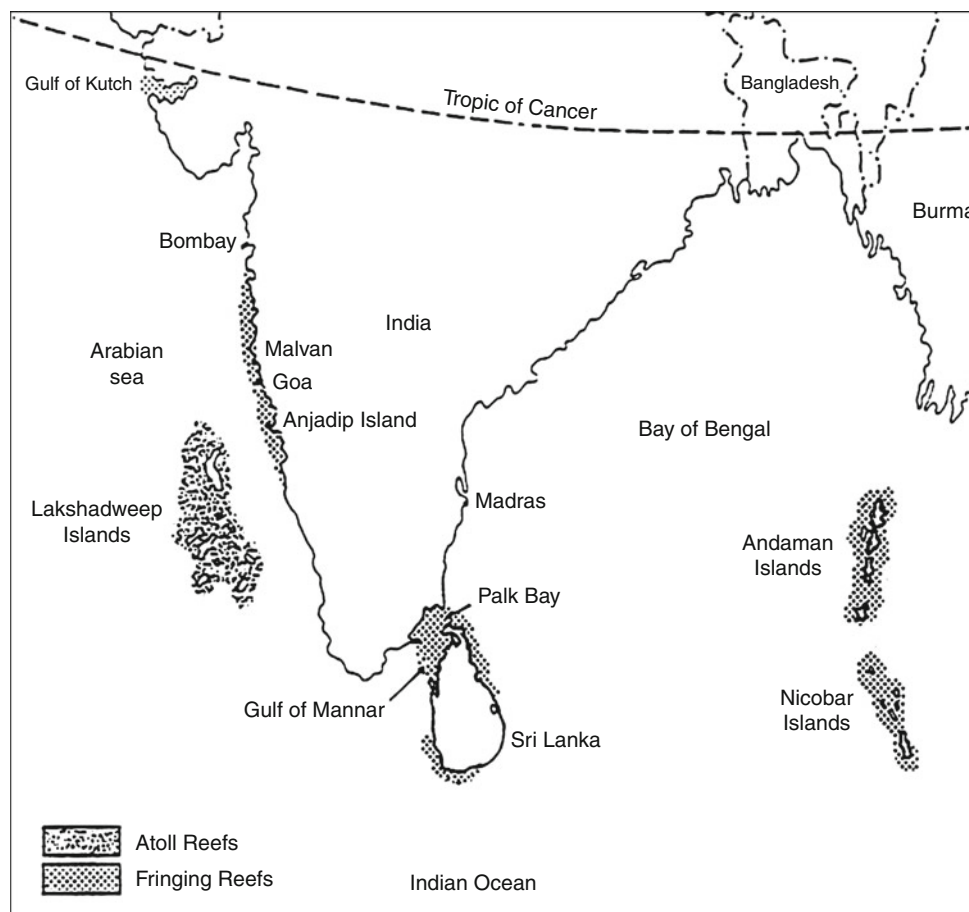
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### Definition and introduction

Coral reefs are one of the most ancient and dynamic ecosystems of India. Coral reefs not only provide a sanctuary to a myriad of marine life but also play a key role in protecting the coastline from erosion. In addition, people living along the 8,000 km long coastal stretch of India depend on coral reefs for their livelihood (Venkataraman and Alfred, 1998, Venkataraman, 2003). India is centrally placed within the warm tropical region of the Indian Ocean and exhibits extensive coral reefs in its marine territories. In India, major coral reef ecosystems are seen in Gulf of Mannar, Gulf of Kachchh, Andaman & Nicobar, and Lakshadweep Islands, which embrace all the three major reef types (atoll, fringing, and barrier) and include diverse and extensive reef areas of the Indian Ocean (Figure 1). Fringing reefs are found in the Gulf of Mannar and Palk Bay. Platform reefs are present along the Gulf of Kachchh. Patch reefs are present near Ratnagiri, Malvan, and Kerala coasts. Fringing and barrier reefs are found in Andaman and Nicobar Islands. Atoll reefs are found in Lakshadweep. Absence of reefs in the Bay of Bengal along the northeast coast is attributed to the immense quantity of freshwater and silt brought by the rivers such as Ganga, Krishna, and Godavari. The total area of coral reefs in India is estimated to be 2,375 sq km.

The studies on the taxonomy of Indian coral reef started as early as 1847 by Rink in Nicobar Islands, and later in 1898, Thurston worked on coral reefs in Gulf of Mannar region. During the whole of twentieth century, many foreigners contributed to coral reef studies in India. Pillai (1983, 1986), the first Indian worker, published many papers on the coral diversity from all the four major coral reefs of India followed by Venkataraman (2003, 2006), Venkataraman and Alfred (1998), and Venkataraman et al. (2003).





**Coral Reefs of India, Figure 1** Major coral reef areas in India.

## Coral reefs: East Coast of India

### Gulf of Mannar

The Gulf of Mannar reefs are found around a chain of 21 islands that lie along the 140 km stretch between Tuticorin and Rameswaram. These islands are located between latitude  $8^{\circ} 47'N$  and  $9^{\circ} 15'N$  and longitude  $78^{\circ} 12'E$  and  $79^{\circ} 14'E$ . The islands lie at an average distance of 8 km from the main-land. They are part of the Mannar Barrier reef, which is 140 km long and 25 km wide between Pamban and Tuticorin. Different types of reef forms such as shore, platform, patch, and fringing type are observed in the Gulf of Mannar (Venkataraman et al., 2003). The islands have fringing coral reefs and patch reefs around them. Narrow fringing reefs are located mostly at a distance of 50–100 m from the islands. On the other hand, patch reefs rise from depths of 2–9 m and extend to 1–2 km in length with width of as much as 50 m. Reef flat is extensive in almost all the reefs in the Gulf of Mannar. Reef vegetation is richly distributed on these reefs. Reef flat and reef vegetation including algae occupies 65 and 14 sq km, respectively (D.O.D and S.A.C., 1997). Pillai (1986) had provided a comprehensive account of the coral fauna of

this region. There are about 94 species of corals belonging to 32 genera in the Gulf of Mannar. The most commonly occurring genera of corals are *Acropora*, *Montipora*, and *Porites*. Extensive sea grass beds are present; green turtles, olive ridley turtles, and dugongs are dependent on these sea grasses as their feeding ground.

### Andaman and Nicobar Islands

The Andaman and Nicobar group of Islands is located in the South East of the Bay of Bengal, between  $6^{\circ}$ – $14^{\circ}N$  latitude and  $91^{\circ}$ – $94^{\circ}E$  longitude. They are the emerged part of a plate edge mountain chain and lie on a ridge that extends southward from the Irrawaddy delta area of Burma, continuing the trend of the Arakan Yoma range.

The Andaman and Nicobar group of islands consist of 530 islands, of which only 38 are inhabited, along with a number of exposed islets and rocks. The principal of these is the North Andaman, Middle Andaman with Ritchies archipelago in the east, South Andaman, little Andaman, Baratang, and Rutland Island. The coral reefs are of fringing type and except for a few investigation reports, the reefs of the area still largely remain unknown.

A deep oceanic ridge along 10°N separates the Andaman Group and the Nicobar group of islands. The orientation of the chain of islands is north-south. In these island groups, there are two Marine National Parks viz., Mahatma Gandhi and Rani Jhansi Marine National Parks. The coral fauna is diverse when compared to other parts of India (Turner et al., 2001).

### West Coast of India

The West Coast of India between Mumbai and Goa is reported to have submerged banks with isolated coral formations (Nair and Qasim, 1978). Coral patches have been recorded in the intertidal regions of Ratnagiri, Malvan and Rede, south of Mumbai (Qasim and Wafer, 1979), and the Gaveshani bank, 100 km west to Mangalore (Nair and Qasim, 1978).

### Malvan

The Malvan coast forms part of the Western Ghats where the Sahyadri ranges gradually meet the Arabian Sea. From Vengurla point, the coast tends towards the north for about 22 km. From Malvan bay, a chain of submerged and exposed rocky islands extends directly south to 15°53'N and 73°27'E. In this chain, several islands exist including Vengurla Rocks at the Southern tip and Sindhudurg Fort at the northern tip. Other small islets around Sindhudurg Fort are Mandel Rock, Malvan Rock, etc. Most of the marine flora and fauna in the intertidal area are exposed during low tide. However, during lowest low tides (particularly negative tides), the coral reefs get exposed. *Porites*, *Coscinaraea*, *Turbinaria*, *Favia*, and *Pseudosiderastrea* are some of the genera reported from this coast (Venkataraman et al., 2003). Siltation is high and salinity may drop to 20 ppt during the monsoons in some habitats, which may restrict the growth of ecologically sensitive forms of ramose corals.

### Lakshadweep Islands

The Lakshadweep Islands lie scattered in the Arabian Sea at about 225 – 450 km from the Kerala coast. Geographically, the islands lie between 8°N–12°3'N latitude and 71°E – 74°E longitude. The islands consist of coral formations built up on the Laccadive-Chagos submarine ridge rising steeply from a depth of about 1,500 to 4,000 m off the west coast of India. The Union Territory of Lakshadweep along with the Maldives and the Chagos Archipelagoes form an interrupted chain of coral atolls and reefs on a continuous submarine bank covering a distance of over 2,000 km. This ridge is supposed to be a continuation of the Aravali Mountain, and the islands are believed to be remnants of the submerged mountain cliffs. There are six tiny islands, 12 atolls, 3 reefs and 5 submerged banks, covering an area of 32 km<sup>2</sup> with lagoons occupying about 4,200 km<sup>2</sup>. Only 11 of the 36 islands are inhabited. Minicoy Island is separated from the rest of the islands by a 180 km wide stretch of sea known as the Nine-degree Channel.

The coral fauna of Lakshadweep is known to harbor 105 species belonging to 37 genera (Pillai, 1996). *Acropora* spp., *Pocillopora* spp., *Porites* spp., and massive and encrusting favids dominate the lagoon and reef flat faunal elements. *Psammocora* spp. are common in the northern islands. There is an abundance of blue coral *Heliopora coerulea*. *Millepora* spp. is dominant in the lagoon. Minicoy has species such as *Lobophyllia* and *Diploastrea* that are common to the Maldives but rarely found in the northern islands. Similarly, the genera *Montipora* and *Echinopora* recorded from the northern group of atolls are not recorded in Minicoy.

### Gulf of Kachchh

Gujarat State has a 600 km long coastline, which is very rich in various edible fishes and various types of algae. The Gulf of Kachchh is the richest source of floral, faunal and marine wealth of India, as it provides favorable conditions for breeding and shelter to all marine life in the 42 islands. The corals in the Gulf of Kachchh survive through extreme environmental conditions such as high temperature, salinity changes, and high-suspended particulate loads. Gulf of Kachchh Marine National Park and Sanctuary is the first National Park in the country (457.92 sq km). The Gulf of Kachchh has the best developed coral reefs along the western coast. Out of the 42 islands in the Gulf, 34 islands are surrounded by fringing or platform reefs. Out of 37 hard coral species reported earlier, only 36 are currently found.

### Geology and geomorphology of Indian coral reefs

Coral reefs characterize an ecosystem of high biological diversity, having the greatest number of species of any marine ecosystem. Coral reefs act as a barrier against wave action along coastal areas thus preventing coastal erosion as well as protecting mangroves and seagrass beds in certain areas, which are the breeding and nursing grounds of various economically important fauna (Venkataraman and Alfred, 1998). However, the processes of erosion, sedimentation, periodic storms, flooding, and sea level change, continually modify the ecosystem. The Holocene transgression, the latest episode of sea-level fluctuations, has left behind many signatures which provide insight into the nature of these changes. Direct and indirect palaeo sea-level indicators (see: [Sea Level Indicators](#)) have been identified with transgressive, regressive or still-stand conditions. These include specific biological indices of corals, molluscs, foraminifers, etc., and certain geomorphological features such as submarine terraces, reefs, notches, raised marine deposits, beach rocks, buried channels, etc (Vora et al., 1996). Glacio-eustatic sea-level fluctuations, along with relief, lithology, sedimentation, tectonic movements, etc., produce depositional and erosional patterns which govern the topography of the continental shelf of the Andaman and Nicobar Islands and other coral reef areas of India (Bruckner, 1988). The topography of the continental shelves where major coral reefs of India are found

(Gulf of Kachchh, Gulf of Mannar, Lakshadweep, and Andaman and Nicobar Islands) is mainly governed by depositional and erosional processes, which occur during glacio-eustatic sea level fluctuations. Other factors involved, directly or indirectly, are structure, lithology, sedimentation, tectonic movements, and climatic changes.

Seismic data from the west coast of India revealed the occurrence of buried reefs off Saurashtra and Ratnagiri, indicating pinnacles and protuberances of different heights. The cliffy coast of southern Saurashtra has preserved a record of the sea level changes during the late Quaternary (Rao and Wagle, 1997). Based on the geomorphic positions of the notches, the older sea strand lies at an elevation ranging from 12 to 15 m above the present BMSL and has been attributed to the last interglacial (MIS-5). Following this, a major tectonic uplift of about 6–9 m was experienced by the southern cliffed coast. The Holocene sea level was recorded at 4–5 m which is about 2 m higher than the general MIS-1 sea level. Thus, the submarine terraces on the shelf must have also been formed during the late Pleistocene to mid-Holocene still stands of the sea level. Radiocarbon dates of surficial samples of algal, oolitic, and coralline limestone (Nair and Hashimi, 1980) collected from the terraces and/or in their vicinity suggest that the innermost terrace along the shelf (55–60 m) is ca 7,845 yrs B.P., and the outermost terrace on the shelf is ca 11,150 yrs B.P.

The distribution of reefs on the west coast shelf is random which perhaps may imply that conditions for reef growth have not been uniform. It is interesting to note that between Mumbai and Mormugao, where the shelf is relatively broader, reefs occur abundantly on the middle and outer shelf. On the other hand, south of Mormugao, where the shelf is narrow, they are sparsely present and only on the outer shelf. Submerged coral reefs may be defined as reefs that were established in relation to a pre-existing sea-level lower than present and occur at depths greater than that commonly associated with vigorous growth of reef building, hermatypic corals. Further, the radiocarbon dating of coral and associated fauna indicates that they are of early Holocene age.

The Lakshadweep Islands rise from a submarine platform with coral reefs in the form of an atoll. It is crescent-shaped having a north-south orientation. The western margin of the lagoon is a submarine bank with a narrow reef below. The lithology is composed of an upper 1–2 m-thick layer of coral rubble, below which is a compact porous crust of conglomerate and soil composed mostly of coral sand. Topography is a flat 1–2 m above sea level. Erosion occurs mostly along the shore towards the northeast and northwest (Anon, 1990).

The Gulf of Mannar extends from Tuticorin to Rameswaram Island in a SW-NE direction and lies between 78°5' & 79°30'E longitudes and 8°47' & 9°15'N latitudes, a distance of about 140 km. There are 21 islands between Tuticorin and Rameswaram. All islands are composed of a calcareous framework of dead reef and sand and have a low and narrow sandy coast.

Around all offshore islands, well-developed coral reefs occur. Geomorphologically, coral reefs in this area are of fringing type, though some patchy corals are also observed in between Appa Island and Pilliyarmuni Island, and in some areas such as the Bharathinagar coast and the southeast coast of Kariya Shuli Island (Loveson, 1993). Wave cut platforms are common on the coast of Mandapam, Ramaswami Madam, Pudumatam, Valinokkam, etc. Along the coast of the Gulf of Mannar, cliffs occur though at some places these features have been destroyed due to slumping. In the Gulf of Mannar, the slope and width of the continental shelf is approximately the same as the average for the eastern coast of India (Ahmed, 1972). The total width of the shelf is around 30 km having a slope of about 21'. The slope near the shore is about 4'. Recent depth contour maps indicate that the seafloor level decreases along the coast and around the islands due to emergence of the land or lowering of sea level (due to tectonism) and sediment deposition. The beach is gently sloping and marked with altered crests and troughs that are formed due to wave action. As the Gulf of Mannar is on the lee side of the northeast monsoon, there is no long-shore drift from the northeast that might affect the morphology of the spit, (Ahmed, 1972). The southwestern shore of Rameswaram has a tongue shaped spit.

The Andaman and Nicobar Islands are parallel to the arcuate plate boundary separating the Indian and Sunda Plates east of the 9°E ridge (Dasgupta and Mukhopadhyaya, 1993; Rajendran and Gupta, 1989). The ridge is believed to have been formed from sediments scraped off the descending Indian Plate interleaved with ophiolites from the ocean floor beneath the Bengal Fan. In that, the islands are bounded to the east by strike-slip faults and spreading centers, and to the west by a subduction zone, the Andaman and Nicobar ridge acts as a small tectonic plate that has been referred to as the Burma Plate by Curray et al. (1982) and as the Andaman Plate by Dasgupta (1993). The geology of the Andamans is described by Oldham (1884) and Tipper (1911).

A series of earthquakes ranging up to a magnitude of 7.5 under the Andaman and Nicobar Islands on 26 December 2004 shook the entire Andaman Sea region. The end result was that the Burma Plate, which contains the Islands, tilted during an earthquake "swarm" lasting for about 8 min after the major quake off Sumatra. Thus, these islands were a source of the tsunamis that spread out across the Indian Ocean and themselves impacted by tsunamis from the whole series of plate movements on that morning. The effects were very different on the mainland of India to the offshore Andaman and Nicobar Islands.

The primary slip offshore of Sumatra was followed by two other slips towards the north. Though some of these findings need to be further substantiated, the fact remains that the Sumatra earthquake caused significant changes to the earth's tectonic processes (Ortiz and Bilham, 2003). The Andaman and Nicobar area, including Car Nicobar, Katchel, and Campbell Islands were not only affected by



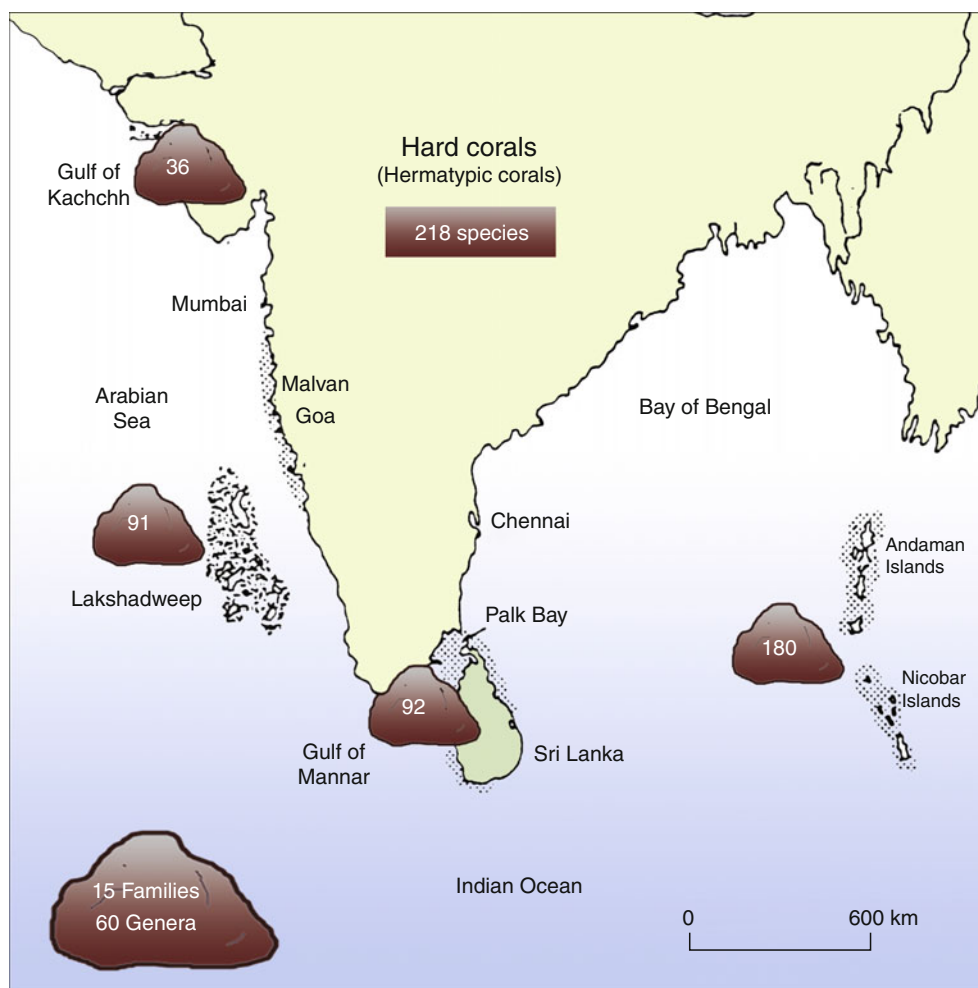
the earthquake but also by the tsunami surge. A subsidence of 1–2 m affected the Nicobar Islands with the maximum down-throw at Indira Point near Great Nicobar. Out of the total area of the Nancowry group of islands, 15.64% of the area has undergone major changes. Nearly 6.8% of the area is submerged and 8.9% of area damaged. Maximum change (more than 42%) has been observed in Trinket Island. More than 23% of Katchall and 9% of Camorta and Nancowry and Tarasa groups have undergone major changes. This resulted in a rise in sea-level, inundating the coastal settlements and narrowing the beaches of the islands. Measurements made at Aerial Bay (Diglipur) and Rangat revealed retreat of sea level to the extent of 1.3 m at Campbell Bay, 1.0 m at Chhattam Island, 0.8–1.0 m in Aerial Bay and 0.4–0.6 m at Rangat. Land surveys at Diglipur and Mayabunder jetties (North Andaman) confirm a vertical uplift of the land up to 1.2 m from the pre-earthquake levels; exposed piles of the jetties, coral reefs and the receded waterline at these jetties stand as testimony to this change (Figure 3).

The coral reefs of Andaman and Nicobar Islands have been damaged by the impact of the recent tsunami and physical removal of other coral reef associated flora and fauna. The tsunami waves increased the sediment load which has smothered and killed sediment sensitive corals and sea grasses. There is significant contamination of coral reefs and coastal waters by run-off from the land, with large quantities of waste and pollutants, debris, soil, and organic matter. Nesting beaches for the five species of globally threatened marine turtles in the Andaman and Nicobar Islands and on the east coast of India have also been damaged.

### Coral reef associated biodiversity

#### Scleractinian corals

Pillai (1983) recorded a total of 199 species divided among 37 genera, from India, which includes Lakshadweep (78 species), the Gulf of Kachchh (37 species), Palk Bay and the Gulf of Mannar (94 species) and Andaman and Nicobar Islands (135 species) (Figure 2). This account



Coral Reefs of India, Figure 2 Diversity Scleractinia in the major coral reef areas in India.



**Coral Reefs of India, Figure 3** The exposed coral reef in the Landfall Island, North Andaman.

includes both hermatypic and ahermatypic corals from the four major coral reefs of India. Venkataraman et al. (2003) identified 15 families, 60 genera and 208 species of Scleractinia (reef building and hermatypic corals) from the four major reefal areas of India such as Gulf of Kachchh (36 species), Lakshadweep (91 species), Gulf of Mannar and Palk Bay (82 species), and Andaman and Nicobar Islands (177 species).

The diversity of scleractinian corals in Gulf of Kachchh is very poor when compared to all the other three major regions of India. Families such as Asterozoeniidae, Pocilloporidae, Euphyllidae, Oculinidae, Agariciidae, Fungiidae, and Trachyphylliidae are totally absent. Species such as *Siderastrea savignayana* and *Acanthastrea hillae* are reported only from Gulf of Kachchh. Twelve families, 34 genera and 91 species are reported from the Lakshadweep Islands. Families such as Asterozoeniidae, Pectiniidae, and Trachyphylliidae are absent. Among the 60 genera recorded in India, only 34 are reported so far from Lakshadweep. Thirteen families, 27 genera and 82 species are reported from the Gulf of Mannar and Palk Bay. From the Andaman and Nicobar Islands, 15 families, 57 genera, 177 species are reported. All the fifteen families reported from India are represented in these islands.

### Algae

Marine algae or seaweeds form an important reef resource in India. A recent publication on the compilation of all the new records of marine algae of India shows that benthic marine algal flora of Indian coasts comprises 844 species under 217 genera including forms and varieties (Oza and Zaidi, 2000). Out of these, the maximum number have been recorded from the Gulf of Mannar (302), followed by 202 species from the Gulf of Kachchh, 159 species from the Malvan coast, 89 species from the Lakshadweep group of Islands and 82 from Goa. In India, seaweeds are exploited and used as raw materials for the production of agar, alginates and seaweed liquid fertilizer. Data on seaweed landings in Tamil Nadu from 1978 to 2000 reveal

that the quantity (dry wt) extracted in a year during this period varied from 102 to 541 t for *Gelidiella acerosa*, 108–982 t for *Gracilaria edulis*, 2–96 t from *G. crassa*, 3–110 t for *G. foliifera*, and 129–830 t for *G. verrucosa* (Ramalingam, 2000).

### Sea grass

Indian coral reefs embrace only 6 genera and 14 species of sea grasses. Distribution of sea grasses along the Indian coast varies with varying species diversity viz. Gulf of Mannar 13 species, Gulf of Kachchh and Lakshadweep 7 species and Andaman and Nicobar reefs 9 species (Kannan et al., 1999). All the 6 genera of sea grasses with 11 species are recorded from the Palk bay region. Of the 11 species, *C. serrulata*, *H. ovalis ovalis*, *K. pinifolia*, and *S. isoetifolium* are the most widely distributed. Out of the 14 species of sea grasses, nine species occur in the Andaman and Nicobar Islands.

### Other marine fauna

Other marine fauna illustrate the great diversity of India's coral reef biota. Some 451 species of sponges from 169 genera have been recorded (Pattanayak and Buddhadeb, 2001). Dominated by Desmospongia, greatest diversity is found in the Gulf of Mannar and Palk Bay. Four turtle species (leather back, Hawksbill, green and Olive ridley) have been observed nesting in the Andaman and Nicobar Islands, (Basker, 1984). Dolphins are common in many areas and dugong in areas of sea grass. More than 1,000 coral reef fish species are found with greatest diversity in the Andaman and Nicobar Islands. There are 3,570 species of marine molluscs (Subba Rao, 1998), almost 3,000 species of Crustacea (Venkataraman and Krishnamoorthy, 1998) and 765 species of echinoderms, 257 in the Andaman and Nicobar Islands alone (James, 1987).

### Threats to coral reefs

Coral reef resources have traditionally been a major source of food for local inhabitants and of major economic value in terms of commercial exploitation. The human exploitation of marine resources has increased dramatically over the last few decades for both reasons of commercial and subsistence living. Coral reef ecosystems of India have been exploited for a very long time, but it is only in the last century that the rate of exploitation has increased dramatically due to the increase in the human population. Except for some of the Andaman-Nicobar Islands, no pristine area exists today.

Varied human activities which are a cause for concern over and above the natural disturbances include, runoff and sedimentation from developmental activities (projects), eutrophication from sewage and agriculture, physical impact of maritime activities, dredging, collecting, and destructive fishing practices, pollution from industrial

sources and oil refineries and the synergistic impacts of anthropogenic disturbance.

Fishing is a major activity, and at present in the 3,651 fishing villages situated along the 8,129 km coastline of India, about one million are occupied in full time marine capture fisheries. The value of the annual marine fish production of 4.6 m t during the year 2002–2003 and the value of marine products export were US \$152.92 m. This is mainly due to the introduction of bottom trawlers, into Indian waters in the early 1960s. Several types of net fishing have also been responsible for the over-exploitation of marine resource. Along with increase in the targeted catch, a number of untargeted fish and other biota are removed from their habitat and discarded as waste (trash fish). Shrimp trawlers probably have the highest rate of by catch bringing in up to 90% more of “trash fish”. A total of 1,006 purse seines in India employed for fishing may have the same effect on the seabed as that of the trawl netting. Random capture techniques employed in India destroy immature fish and other non-targeted marine species. Gill nets used to catch fish bring in a host of other animals such as dolphins, turtles, *etc.* Because of the large size of the areas concerned (Gulf of Mannar and Andaman and Nicobar Islands or other areas in India), and the general lack of resources for enforcement, awareness education appears to be more successful than legislation in controlling these activities.

Although now illegal, blast fishing has been a widespread fishing technique in India. Schooling reef fishes are located visually, after which the capture boat moves within close range and a lighted bomb is thrown into the middle of the school. Due to blasting, branching, tabulate and foliose hard corals are shattered while massive and columnar corals are often fractured. Bombs made of chemical fertilizers such as ammonium/potassium nitrate were confiscated from the foreign poachers apprehended in Andaman and Nicobar Islands. Gelatin sticks were observed to be used to blast fish by the fishermen around Gulf of Mannar reefs (Venkataraman et al., 2003).

Sedimentation throughout the coast of India physically interferes with the recruitment of coral larvae, which require a solid substratum upon which to settle and metamorphose. Illegal sand mining in Andaman Islands and illegal coral quarrying in Gulf of Mannar (Tuticorin group of Islands) and some islands of Gulf of Kachchh have caused a lot of sedimentation and siltation on coral reefs.

There has been unprecedented bleaching of hard and soft corals throughout the coral reefs of the world from mid 1997 to late 1998 (Wilkinson, 1998, 2000). Most of the corals in the coral reefs of India have been adversely affected during the bleaching in 1998, which destroyed most shallow water corals. This event has greatly reduced live coral cover in the reef (Venkataraman, 2000). Study conducted after or during the bleaching event reported a reduction in live cover of corals in Gulf of Kachchh (20–40%), Gulf of Mannar (20–40%), Lakshadweep (20–30%) and Andaman and Nicobar Islands (<10%).

The live coral cover in Andaman and Nicobar Islands was between 50–75%, which is very high when compared to other reefs in the Indo-Pacific region (Muley et al., 2000, Rajasurya et al., 2002).

In addition to natural and human induced coral degradation, coral diseases are considered to be one of the major problems faced by the coral reefs in recent years. Necrotic lesions, fleshy algal over-growth, black band disease, and white band disease have been reported from the Andaman and Nicobar and Lakshadweep Islands. In addition, a new disease called pink line disease has also been reported recently from Lakshadweep (Ravindran and Raghukumar, 2006).

The coral eating starfish, *Acanthaster planci* was the focus in the late 1980's and early 1990's in the Andaman and Nicobar Islands as well as in other coral reef areas of India (Venkataraman and Rajan, 1995). Although sediment core data have indicated *Acanthaster* outbreaks 10,000 years ago, recent studies have shown a relationship between nutrient input and recruitment success of the larvae. Studies on echinoderm reproduction have demonstrated that the success of the recruitment of their planktonic larvae depends on phytoplankton availability following spawning.

#### Coral damage from the Tsunami of 26th December, 2004

The major damage to reefs is caused by storms, particularly tropical cyclones and by tsunami. These cause major intermittent damage to reefs, particularly to those reefs that rarely experience these storms. Due to a 1969 cyclone, a large area of coral was buried under sand in the Rameswaram area of the Gulf of Mannar. Likewise, the cyclone of December 1987 in the Bay of Bengal devastated the coral reefs of the Mahatma Gandhi Marine National Park of Port Blair, Andaman that resulted in piles of broken coral colonies scattered near the shore.

A very severe earthquake with a magnitude of 9.0 on Richter scale struck northern Sumatra, Indonesia on 26th December, 2004, and it was widely felt along the east coast of India. In Tamil Nadu, people felt distinct tremors in many parts of Chennai. The quake was also felt along the Coromandel Coast up to some areas in Vizakapatnam. The devastating tidal waves consequent to the earthquake lashed several coastal districts of Tamil Nadu and Puducherry as well as the archipelagos of the Andaman and Nicobar Islands. The Nicobar Islands were most severely hit given their proximity to the island of Sumatra and the epicenter of the earthquake. It is reported that shallow water coral reefs in the Andaman Islands have been exposed 2 m above the water mark (Figure 3) whereas the Nicobar group are submerged 2.0 m below the water mark (Venkataraman, 2006).

#### Conservation

India has 36 marine protected areas of which 20 are entirely located in intertidal/subtidal or seawater-mangroves, coral



reefs, lagoons, estuaries, beaches, etc., and 13 having major parts in marine ecosystem and some part in terrestrial ecosystem (Singh, 2002). The Wildlife Protection Act, 1972 provides protection for these areas and certain marine species. Corals are protected under this act. India's Coastal Regulation Zone Notification (1991) regulates onshore development activities, which affect coastal environments. Coral reef conservation is also included in the Environmental Protection Act (1986), the National Conservation Strategy and Policy Statement on Environmental Development (1992) and the Action Plan of the Ministry of Environment and Forests.

## Conclusion

Coral reefs in India have drawn great attention from the eighteenth century onwards. This was achieved from many surveys and expeditions conducted by foreigners, in particular by the British. The introduction of Surgeon Naturalists in the expedition ships helped marine research to flourish in varied fields of fauna and flora. However, in India, major studies have been conducted only on the commercially important organisms such as crustaceans, molluscs, holothurians, and higher vertebrates. Many minor phyla which are not commercially important have not been studied so far. For example, species of different minor phyla that live as the interstitial fauna of coral reef areas have not been studied till date, due to a lack of expertise in this field. Though taxonomy is being taught as a subject in the curricula of schools and colleges, there is no committed institution for the learning of taxonomy except survey departments under the placard of the Government of India. Probably, more than 75% of the biodiversity of coral reefs of the Andaman and Nicobar and Lakshadweep is not yet studied. This is mainly attributed not only to the decline in the number of taxonomists but also due to the lack of facilities. Geological and geomorphological studies are probably even less advanced which is unfortunate given the wide geographical distribution of coral reefs in India.

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## Cross-references

[Eastern Indian Ocean – Northern Sector](#)  
[Indian Ocean Reefs](#)  
[Maldives](#)  
[Tropical Cyclone/Hurricane](#)  
[Tsunami](#)  
[Western Indian Ocean](#)

## CORALS: BIOLOGY, SKELETAL DEPOSITION, AND REEF-BUILDING

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### Definition

Scleractinian corals (Phylum Coelenterata, Class Anthozoa, Order Scleractinia – the true stony corals alive today) have been building coral reefs for 250 million years, reefs that are the biggest structures ever made by living organisms.

### Introduction

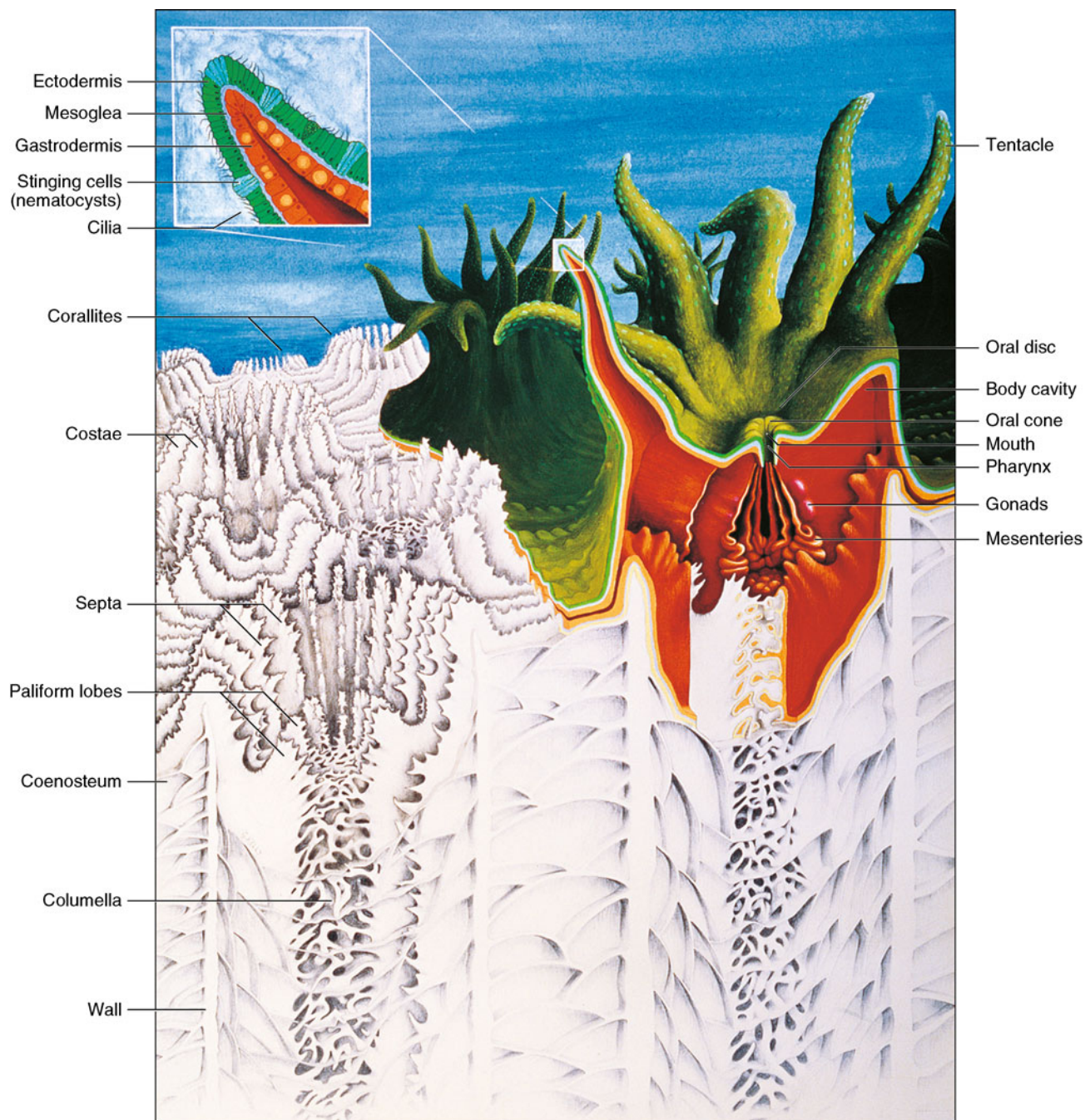
Scleractinian corals have a simple structure. Their bodies are sac-like polyps that usually grow together to form colonies. They have a body wall with only two cell layers and a skeleton made of calcium carbonate which is actually outside their body so that the living polyp grows on its skeleton (Figure 1). This simple structure allows most corals to form complex colonies that are readily modified to suit a wide range of environments. Modern coral reefs are principally made of calcium carbonate that has been derived from coral skeletons and cemented into a wave-resistant structure by coralline algae (see [Coral Reef, Definition](#)). Whereas coralline algae generally have a wider distribution range than corals, both flourish in shallow, turbulent, well-lit environments, which is where highly consolidated reefs best grow. Growth rates of coral colonies and of reefs are very different and are discussed below: coral growth rate is a result of each colony's individual physiological performance within its particular environmental setting and reef growth is a net outcome of history, hydrodynamics, ecosystem processes, and the functional roles of various guilds of species – both constructive and destructive. Moreover, there is wide diversity of entities referred to as “reef,” with the contribution of corals likewise varying in importance: these are reviewed briefly here.

### Reefs and coral reefs

The term “reef” can mean different things to different people. To most geologists and palaeontologists, reefs are rock formations. To most biologists, reefs are a veneer of living organisms forming an ecosystem, which is both complex and fragile. These two concepts of reefs can seem as remote from each other as forests are from coal deposits, yet they share a common past. Reefs, the geological structures, are the direct products of living ecosystems and as such their formation has always been controlled by the sorts of events that control other ecosystems, both marine and terrestrial.

When considering ancient reefs, it is important to distinguish these “reefs” from the “coral reefs” of today. Corals are not the main builders of all reefs: many ancient reefs, especially those of the Palaeozoic, were not built just by corals but by a wide array of other taxa including





**Corals: Biology, Skeletal Deposition, and Reef-Building, Figure 1** The general structure of a coral polyp and underlying coral skeleton (After Veron, 2000).

algae, sponges, and molluscs. In many Palaeozoic reefs, sponges rather than corals were the dominant builders and in some late Mesozoic reefs, the same role was played by molluscs (rudist bivalves).

Even modern reefs are not necessarily coral dominated. Some, forming intertidal structures in the Caribbean and Bermuda, are made by vermetid “worms” (molluscs). There are also widespread subtidal structures dominated

by serpulid worms (annelids) and odd reefs everywhere owe their existence to other organisms, especially oysters. However, in terms of quantity, the reefs dominated by organisms other than scleractinian corals and their allies (including a few small taxa such as the blue coral *Heliopora* and the fire coral *Millepora*) are insignificant and have little in common with coral reefs other than in the material of which they are made. Such structures



excluded, the term “coral reef” still needs constraining, for some deep ocean corals form extensive structures, built by one type of coral (*Lophelia*). These are commonly called reefs, but they have none of the characteristics of coral reefs as geological structures (they do not form solid limestone) or as biological structures (they do not depend on photosynthesis nor are they biologically diverse).

There is one further distinguishing characteristic of coral reefs: although they are principally made of calcium carbonate derived from coral, coral skeletons need to be cemented into solid rock by coralline algae. Coralline algae generally have a wider distribution range than corals, but those that cement coral debris into reefs flourish in shallow, turbulent, well-lit environments and thus it is they as much as corals that determine where highly consolidated reefs best grow. They may also have a dominant influence on how fast they grow or if they grow at all in deeper water.

### Reef carbonates

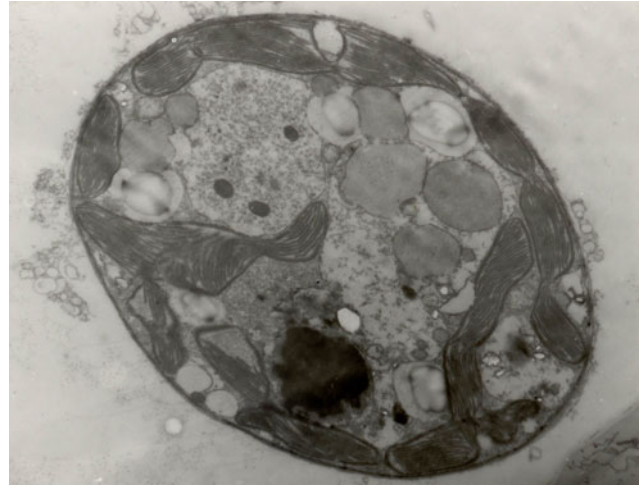
Although most (90–95%) of terrestrial limestone is derived from reefs built by a variety of animals in shallow marine environments, this by no means reflects the principal source of carbonates on Earth. Around 90% of all today’s marine carbonates are deep-sea sediments derived primarily from plankton (mostly foraminifera and coccolithophores). Due to their deep water location, these are rarely uplifted to form geological rock formations on land; rather they are either dissolved in the ocean or subducted into the Earth’s mantle. Another 5% of carbonates are of mixed composition and are found on continental slopes. In a few regions, these carbonates have been consolidated and uplifted or otherwise exposed on land.

Perhaps surprisingly, only 5% of all carbonates today are of coral reef origin although this small proportion includes vast tracts of mountain slopes like the calcareous reefs of Austria. The proportion of total carbonates which are represented by living reefs is much less than 1%. Nevertheless, this small proportion is all important.

### Reef building

If corals grow in sufficient quantity, and the rate of both skeleton production (calcification) and algal cementation exceeds that of erosion, the resulting accumulation of calcium carbonate can form limestone reefs. The success of the process depends on speed, which is why reef-building corals enlist symbiotic algae (zooxanthellae, [Figure 2](#)) to harness the energy of the sun to power the process. This begs the question, why do these organisms put so much metabolic effort into reef-building? After all, no other ecosystem in all Earth’s history puts anything like as much energy, or such evolutionary focus, into building anything that is dead.

One answer lies in the purpose of skeleton building. Only corals that build reefs have large, three-dimensional, wave-resistant skeletons. This capacity has been achieved by removing the limitations of individuals and replacing



### Corals: Biology, Skeletal Deposition, and Reef-Building,

**Figure 2** An electron microscope image of a zooxanthella. This tiny cell, 10  $\mu\text{m}$  in diameter, has all the structural components of a typical algal cell (Electron microscope image: Ove Hoegh-Guldberg).

them with a wider range of options offered by the formation of colonies (groups of individuals formed asexually and which grow in unison). The implication is that skeletons are needed to form colonies and that colonies are needed to build large wave-resistant structures.

The two evolutionary innovations of colony formation and algal symbiosis clearly go together and have very likely evolved together. The importance of this is demonstrated by the fact that most Cnidaria involved in reef-building are both colonial and symbiotic. The two major groups of extinct reef-building corals (rugose and tabulate corals) are also colonial; however, it is not known if they were also symbiotic.

Coral reefs are ecosystems, which mean that they are not just aggregations of individual species competing with each other for survival, but rather groups of species living cooperatively for joint survival. Certainly individual species compete; however, a level of selection takes place which is higher than the selection of species. From a Darwinian perspective, this might be called “selection for survival of the fittest ecosystem” as opposed to selection for the fittest species. Where there is a close symbiosis between two species, the evolutionary success of one species is dependent on that of the other: natural selection acts on the partnership, not the species. A coral reef has hundreds of such interdependencies, resulting in a complex coevolution of subcomponents and entire ecosystems.

This introduces the concept of guilds (Bellwood et al., 2004), where each guild is a functional unit whose task is undertaken by a group of species or individuals. All coral reefs have many guilds including corals (to produce building blocks), coralline algae (to cement the blocks together), herbivores (to prevent macroalgae from taking over), and photosynthetic algae (to provide food). There

are also less prominent guilds, forming a hierarchy down to less conspicuous tasks such as parasite control, sediment mixing, and nutrient cycling. The essential point about guilds is that they are functional units selected for because they perform functions efficiently. It matters little what species perform the function, only that they do it with the necessary speed.

Corals are the most prominent reef-builders today because, with their zooxanthellae, they can harness the energy of sunlight to make building blocks sufficiently quickly to outstrip erosion. This is not to say that all zooxanthellate corals contribute to reef-building; perhaps half of all species make no significant contribution to reefs at all for they do not grow in environments suitable for reef growth, especially where the water is too turbid or too cold or where there is limited hard substrate, or because their skeletons are fragile and are easily removed by wave action.

The reason why corals build reefs has as much to do with the physical environment as with organisms: it is a matter of ecology.

### Light

Reef-building corals depend on photosynthesis for they use the unlimited resources of solar energy and air to produce food. However, about half of all Scleractinia (the azooxanthellate species) do not have symbiotic algae. Some azooxanthellate corals live on coral reefs, especially under overhangs or in caves, but with the exception of a few species that are both symbiotic and nonsymbiotic, all zooxanthellate corals need light, and it is only these taxa that build reefs. As a result, reefs are restricted to shallow sunlit waters. Azooxanthellate corals are not limited by light or by temperature, nor are they confined to shallow sunlit water; they live in the ocean depths where there is less competition for space. Therefore, they cannot build reefs and must live without food from photosynthesis: food can only come from detritus and the chance of capturing passing plankton.

### Algal symbiosis

Symbiosis, the interdependence of different organisms for the benefit of one or both participants, is much more prevalent in the oceans than on land. Within the spectrum of symbioses, zooxanthellae clearly have a special place. They are not just found in Scleractinia; they occur in other cnidarians (soft corals, anemones and their allies) as well as in an assortment of other animals including single-celled ciliated protists, sponges, flatworms, and molluscs (including giant clams). Once thought to be a single species, zooxanthellae have been found to be genetically diverse (consisting of many genetic types or “clades”) (Trench, 1979; Rowan and Powers, 1992), even though under a microscope they all look much the same (Figure 2). They can all live independently, although not in such concentrated numbers nor with such long-term security as they can live in the tissues of hosts. In the case of corals (but not clams), they live inside the cells of the

host organisms – in the innermost (gastrodermal) layer of the two cell layer body wall (illustrated above). All zooxanthellae are tiny, around one hundredth of a millimeter in diameter. Seldom does more than one occur in a single gastrodermal cell.

Zooxanthellae photosynthesize as do other green plants, releasing up to 95% of the nutrients they produce to the host organism (Muscatine, 1990). This is a curious arrangement because most corals are voracious feeders on zooplankton and therefore have two very different food sources. Nevertheless, many if not most corals that are kept in darkness (so that their zooxanthellae cannot photosynthesize) will start to die after a few months no matter how much food they have. Somehow, the zooxanthellae have made themselves indispensable. Just how or why remains unresolved.

In brief, important points about algal symbiosis are as follows (Hoegh-Guldberg, 1999 and many subsequent articles). Corals acquire their zooxanthellae either directly from the parent colony or through infection of free-swimming or newly settled larvae. Uptake of nonparental zooxanthellae in early life may be by random chance, giving different advantages to different colonies: some colonies might be infected with temperature-tolerant symbionts, others with more productive ones (this hypothesis has yet to be confirmed). Zooxanthellae readily change in abundance depending on conditions such as season, position on the coral, and light level. More than one genetic type of zooxanthellae can occupy a single colony. The abundance of genetic types varies geographically on any scale (Ulstrup and Van Oppen, 2003) and some genetic types facilitate a faster growth rate than others (Little et al., 2004).

### Water depth, turbidity, and latitude

Any factors which alter light in the marine environment will have a significant effect on calcification rates and reef development. Depth is a primary constraint as only a few zooxanthellate corals live below 100 m, even where the water is very clear and the substrate does not slope so steeply that it is shaded. *Leptoseris* commonly forms extensive beds to at least 160 m in the Red Sea and Hawaii, and there are several records of moderately diverse coral communities at depths of over 100 m elsewhere, including the outermost reef faces of the GBR.

Turbidity has a dominant role to play in controlling light levels in all except clear-water habitats. Where the water is not very clear, as is the case with most reefs near major land masses, coral diversity drops off sharply at depths below about 50 m. Where the water is particularly muddy, the depth limit for any coral can be as little as 5 m. Turbidity, especially that caused by fine clay particles which are easily resuspended by wave action, has other effects on corals besides reducing light.

Latitude also has an effect on light availability, much more in the ocean than on land due to the refraction of sunlight as it enters water. The higher the latitude the

shallower coral communities must be in order to have adequate light. This is of less consequence today than in past geological intervals when waters were warm enough for reef-building to occur at high latitudes, even as far as the Arctic and Antarctic circles.

### Temperature

Temperature, in synergy to some extent with light, sets limits on the latitudinal spread of corals throughout the world. A different temperature constrains the spread of reefs. The difference between these two – constraints on corals and on reefs – has created havoc in palaeoclimatic reconstructions of past reef environments as well as studies of reef growth because it is so widely misinterpreted.

#### Low-temperature limits to reef growth

It has been known for decades that reefs do not form where the ocean temperature regularly goes below 18°C for intervals of weeks to months. Reef geologists concerned with the history of reefs refer to this well-established fact, yet in so-doing they often assume that lower temperatures kill corals. This is seldom the case.

As noted above, reef-building allows entire ecosystems to exist, a process that can only happen if rampant growth of macroalgae is held in check (Crossland, 1988). This requires a great deal of uninterrupted energy, which is why reef-building corals are so dependent on symbiotic algae. We have also seen that this symbiosis requires exposure to sunlight, which means living in shallow water. Around 18°C corals are able to produce calcium carbonate fast enough to fulfil their guild role as producers of building materials. They are able to do this not by growing faster than algae, but by creating three-dimensional habitats where herbivores, especially fish, can control algae for them. At lower temperatures, algae usually get the upper hand; however, the corals themselves are not affected by temperatures lower than 18°C. This is best seen along the Ryukyu Islands of Japan where the southern islands have extensive reefs, yet further north the sea temperature progressively decreases until it reaches the critical 18°C point. It is here that reef development fails. The corals, however, do not: nearly half of all coral species regularly tolerate prolonged exposure to 14°C (Veron and Minchin, 1992). A few tolerate 12°C although seldom less (azooxanthellate corals excepted).

#### High-temperature limits to reef and coral growth

Low- and high-temperature limits do not mirror each other. Oceans can cool until they freeze, yet they cannot warm much beyond the peak temperatures we see today (around 31°C). This is because evaporation holds the upper limit in check, at least it does for extensive areas of ocean. Smaller bodies of water are less constrained, thus, reef lagoons can get at least 5°C warmer than this. Nevertheless, high temperature per se has little direct negative effect on corals. The warmer the water the faster most metabolic processes become and the faster calcification could become

if it were not for its effect on zooxanthellae. Faster metabolic rates for zooxanthellae mean faster photosynthesis, which in turn can result in oxygen being produced at rates where it becomes toxic. Corals are forced to expel their increasingly poisonous zooxanthellae and “bleach” in response to temperature and light acting in concert.

High-temperature limits of coral growth and reef growth are approximately the same as they are both linked to the upper limit of the ocean. This link is an evolutionary one and appears to have always existed for there is no interval in geological time where high temperature has excluded reefs from equatorial regions.

#### Substrate, turbulence, and mechanical effects

Substrate type and water clarity are always closely linked, especially when depth and turbulence are factored in. White calcareous sand, although typically coarse-grained, is light and therefore readily moved around by wave action, in which case it is capable of burying corals if suspended in sufficient quantity. However, it is clay from rivers that adversely affects corals, for not only does it attenuate light, but it also requires cleaning, a costly activity in terms of metabolic energy.

Substrate is also of paramount importance to settling larvae, for these will not settle on sand of any sort, or on substrates that are coated with bacterial slime, as it commonly develops on reefs that have been degraded.

One very obvious effect of turbulence on coral skeleton formation is that wave action produces dense skeletons. Corals in a high-energy environment grow dense skeletons, whereas those in protected areas have light, brittle skeletons. This is partly because of the differences in species that occupy these habitats, yet even within the same species this effect is pronounced.

#### Water quality

The term “water quality” is commonly used in connection with the health of the marine environment. Water quality that is good for particular coral reefs or coral communities is assumed to have tolerable levels of sediments and nutrients and environmental contaminants.

Salinity is an aspect of water quality that has not been adequately studied. Corals appear to be sufficiently tolerant of high salinity that lethal levels seldom, if ever, occur naturally. The opposite commonly applies to low salinities, for these play a large role in creating areas where there is little or no coral or reef growth.

There are other environmental controls on reef-building hidden in water chemistry that may not overtly limit reef distribution today but which may have been important in the geological past and are destined to become so in the near future. Oceans are normally so well buffered that chemical changes are infinitesimally slow, providing plenty of time for organisms to evolve adaptations to any alteration. However, sometimes the rate of change exceeds physical or biological thresholds and cannot be tolerated by any except the most specialised organisms. This can



happen when large tracts of ocean become anoxic, hydrogen sulphide concentrations become toxic, pH alters beyond tolerable limits for calcification, or other contaminants make the water uninhabitable.

### Rates of growth and erosion

Growth rates of coral colonies and of reefs are very different subjects because (1) reefs are made of a much denser material than are coral skeletons, (2) there are gaps between coral colonies that must be in-filled to make solid limestone and (3) reef accretion is the rate of growth minus the rate of erosion – the latter is commonly greater, especially in marginal habitats. This is the main reason why reefs do not form wherever coral grows.

### Coral growth rates

The much-studied coral *Porites* forms large hemispherical colonies which typically grow (radially) at a rate of around 1 cm per year as determined by X-rays of thin slices (Figure 3). Some more heavily calcified colonies of other corals grow at slower rates than this, although most are faster. Staghorn *Acropora* readily grows (linearly) up to about 30 cm per year. Plate-forming *Acropora* also grows (in diameter) up to about 30 cm per year.

### Reef growth rates

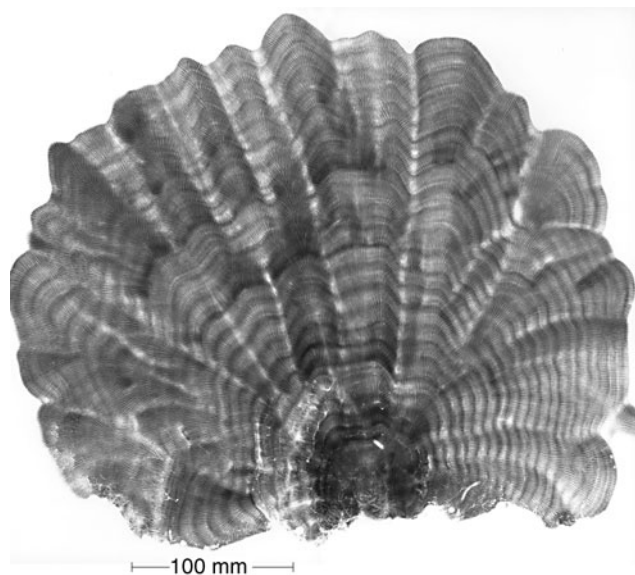
Rates of growth of reefs (accretion) can be measured directly from cores taken from reefs or by a wide range

of indirect measures of carbonate production (Vecsei, 2004). Normally, the maximum rate of reef growth is about 0.6 m per century (Smith, 1983), although rates in optimal conditions may reach three times this (Montaggioni, 2005; Hopley et al., 2007). These optimal conditions only occur where the water is shallow and clear and currents are strong, the probable reason why continuous areas of reefs (where there is more reef than open ocean) occur only where the tidal range is great and the ocean floor is shallow. These environments provide high light levels combined with continuous flushing and nutrient transport.

### Rates of reef erosion

There are no reliable estimates of rates of reef erosion because they are too slow to be directly measurable. Best estimates suggest that around 90% of all calcium carbonate produced by coral calcification is removed by erosion. There are four main mechanisms of reef erosion: physical erosion, enhanced chemical erosion, bioerosion, and rain-water dissolution.

1. Physical erosion leads to the formation of channels seen in most reefs due to the action of waves moving rubble back and forth. These channels typically develop into “spur and groove” structures common along most reef fronts exposed to strong wave action. On a bigger scale, erosion caused by tidal currents may produce “deltaic patterns,” so named because they resemble river deltas.
2. Changes in ocean chemistry which affect the stability of skeletal material can have a significant effect on the balance of reef accretion and erosion. Ocean acidification, predicted to occur during the present century, will bring this subject to the forefront.
3. Bioerosion is a greatly underrecognized process, yet can be very active in shallow water where it not only erodes the limestone surface but also prevents the growth of newly recruited corals and coralline algae on available substrates. Over thousands of years, the actions of many types of bioeroders, such as the urchins, would probably be capable of keeping pace with slow sea-level falls, or successions of slow falls, and therefore would leave no reef exposed above high tide level. There are many studies of the rate at which different organisms (such as sponges, urchins, limpets, chitons, and parrot fish) ingest limestone (typically up to 18 cm<sup>3</sup> per animal per year for intertidal invertebrates such as sea urchins); however, these cannot be reliably translated into rates at which these animals might plane-off whole reef surfaces.
4. Rainwater dissolution commonly results in “rill weathering,” a process that creates interlocking knife-like edges on the surface of limestone outcrops. Depending on the chemical composition of the limestone, some aerially exposed reefs last much longer than others, as evidenced by the ancient reefs that remain intact today.



**Corals: Biology, Skeletal Deposition, and Reef-Building, Figure 3** Growth bands in corals such as seen in this X-ray of a slice of *Porites* are the marine equivalent of growth rings in trees. They not only allow detailed measurements of growth rates, but can also reveal much about the environment in which the coral grew, including temperature and salinity (X-ray image: Janice Lough).

An important point about these forms of erosion are that the first three occur only when reefs are submerged, while the fourth occurs only when reefs are exposed to the air, either by uplift of the land or by falls in sea level.

## Summary

The subject of coral skeleton formation has two separate aspects, reef building and coral growth. Reefs are both geological structures and living ecosystems. Corals are often not the primary builders of Palaeozoic reefs, thus the terms “reefs” and “coral reefs” are not necessarily interchangeable terms in geological contexts. However, scleractinian corals are the builders of most Mesozoic and Cenozoic reefs. The environmental controls on both are similar, not necessarily the same.

The two great scleractinian innovations of colony formation and algal symbiosis allow corals to build reefs. These are closely linked, both functionally and in evolutionary terms. Light and temperature are the dominant parameters.

Light availability is critical for reef-building because of the dependence of corals on algal symbiosis. In turn, light availability is regulated by water depth, turbidity and (in geological time) latitude.

Temperature limits the latitudinal distribution of reefs and constrains the rate of skeleton formation. For ecological reasons, reef formations are limited to oceans that do not cool below 18°C for extended periods of time. However, most corals can grow where temperature commonly falls to 14°C. High-temperature limits to both reef growth and corals are similar, approximately 31°C.

Rates of coral and reef growth are very different. Rates of coral growth vary enormously according to the type of colony formation. Rates of reef growth are dependent on rates of erosion. This occurs by four processes, physical erosion, changes in water chemistry, bioerosion and rain-water dissolution.

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## Cross-references

[Acropora](#)  
[Algae, Coralline](#)  
[Algae-Macro](#)  
[Aragonite](#)  
[Coral Reef, Definition](#)  
[Corals: Environmental Controls on Growth](#)  
[Ecomorphology](#)  
[General Evolution of Carbonate Reefs](#)  
[Ocean Acidification, Effects on Calcification](#)  
[Sediment Durability](#)

## CORALS: ENVIRONMENTAL CONTROLS ON GROWTH

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 Australia

## Definitions

**Coral growth:** The establishment, survival, and increase in size of living zooxanthellate corals as individuals, populations, and communities.

**Coral calcification:** The biological process of the synthesis of calcium carbonate by corals. Its rate is reported in  $\text{gm cm}^{-2} \text{ year}^{-1}$ . A given rate of calcification is manifest in a coral skeleton as its rate of linear extension ( $\text{cm year}^{-1}$ ) of a particular density ( $\text{gm cm}^{-3}$ ).

**Environment:** The physical, chemical, nutritional, and ecological milieu in which corals grow.

**Microenvironment:** “Environment” impinging upon an individual coral in situ.

## Introduction

Corals grow vigorously and build reefs in shallow tropical seas, due to the favorable environment, both “latitude-correlated environmental factors” (Veron, 1995) and factors that are not related to latitude. The latitude-correlated environmental factors are solar radiation, temperature, and water chemistry (Kleypas et al., 1999), and those not related to latitude include nature and depth of the substratum, wave climate, salinity, water clarity, nutritional properties of that water, and sedimentation regime. Collectively, they affect growth rate, growth form, reproduction and longevity of individual corals, the trajectories of abundance, size and age-frequency distribution and turnover rates of populations, and the composition and diversity of coral communities. These population and community attributes in turn influence the frequency and amounts of calcium carbonate skeletons that can be delivered to, and accumulate in, reef-building units (framework, boulders, blocks, rubble, and sand) – i.e., contribute to the growth of maintenance of a coral reef and adjacent sedimentary deposits against disaggregating forces of waves, currents, and gravity in shallow tropical seas.

Just as important as the normal fair-weather environment in determining a coral community’s extent and structure are the legacies of their history of development, disturbance, and recovery. Coral communities (see *Coral Reef, Definition*) are all works in progress – outcomes of the timing and makeup of successive settling cohorts of coral propagules (larvae and fragments) and a long list of species-specific differences among corals: their performance in competition with other benthic organisms trying to occupy the same piece of substratum (corals, other sessile invertebrates, and algae); attractiveness or resistance to predators and diseases; susceptibility to breakage or dislodgement by storms; propensity to collapse under their own top-heavy weight and fall off the reef into inhospitable depths; propensity to be dislodged, swept, rolled, or pushed from the area by waves and currents.

## Coral: the animal–plant symbiosis

Underpinning the coral vigor that builds reefs in tropical seas is the presence of hundreds of thousands of “zooxanthellae” (single-celled dinoflagellate algae in the genus *Symbiodinium*) within every square centimeter of the coral’s tissues (Fagoonee et al., 1999; Fitt et al., 2000). Corals that host zooxanthellae are referred to as “zooxanthellate” corals. Within its diurnally and seasonally variable external environment, the coral needs to provide an internal environment that nurtures the zooxanthellae. Whereas corals generally live for decades to centuries, the zooxanthellae populations and coral tissue in which they reside turn over on time scales of weeks to months (Fitt et al., 2000). Under extreme environmental stress, the coral’s internal environment can become inhospitable and zooxanthellae populations may crash and the coral tissue get damaged, leading to injury or death

of entire coral colonies across vast areas (see *Climate Change and Coral Reefs*).

Within coral’s favored environment, the symbiotic arrangement between the coral “host” and its zooxanthella “symbiont” provides such a hospitable intracellular environment for the symbionts that their photosynthesis produces a massive surplus of energy-rich compounds (Gattuso et al., 1999). These are used by the coral polyps to fuel their replication and to deposit their shared skeleton. The rate of calcification (see Definition above) in zooxanthellate corals far exceeds that which is possible in cnidarians that lack zooxanthellae: their presence drives “light-enhanced” calcification (Goreau and Goreau, 1959). However, one decade into the twenty-first century, the coral–zooxanthellae symbiosis, in existence since the Tertiary and critical for the development of coral reefs (Stanley and Swart, 1995), faces increasing incidence and severity of both sublethal stresses and lethal extreme events. Recent reviews of implications of global climate change for corals and reefs include Done (1999); Buddemeier et al. (2004); Chadwick-Furman (2006); Kleypas and Langdon (2006); Guinotte and Fabry (2008); and Veron (2008). See also below in this article and the Chapter on *Climate Change*.

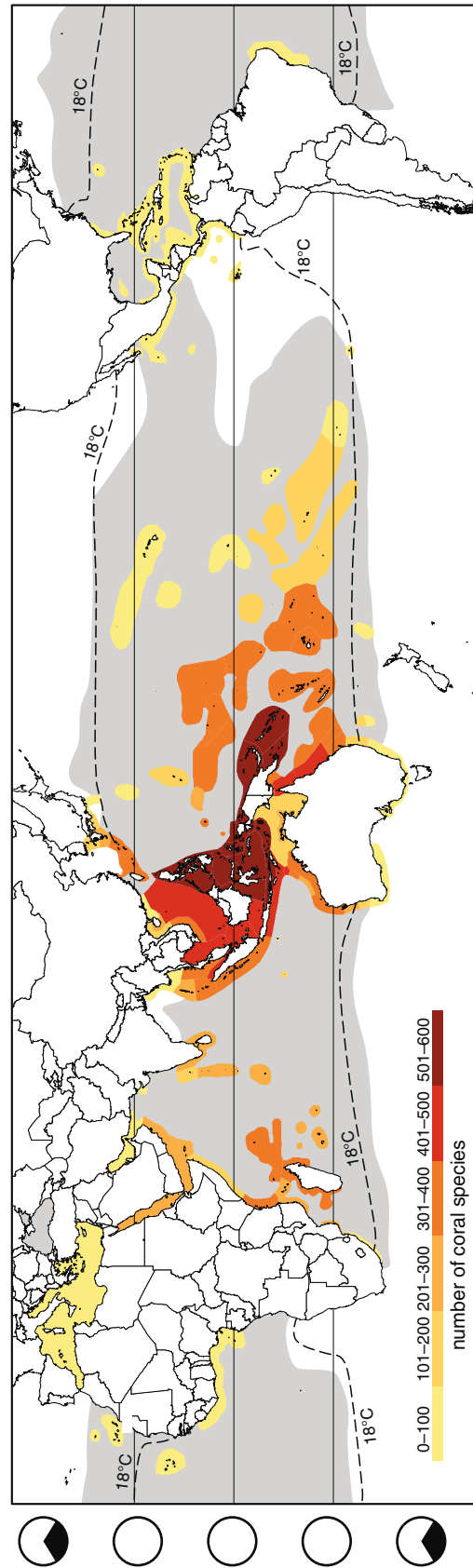
## Environmental controls on global distribution of corals

Today’s global coral distribution (Figure 1) is in part, a legacy of earlier dispersal and establishment processes (Veron, 1995) and in part, a reflection of habitability constraints imposed by the present day environment, notably, those affecting coral’s capacity to calcify. Light-enhanced calcification requires a particular regime of water chemistry, temperature, and solar radiation. Globally, the coral regions of the world have been ranked along a spectrum of environmental suitability for coral calcification – from “optimal” to “marginal” (Kleypas et al., 1999; Guinotte et al., 2003). Seas with an aragonite saturation ( $\Omega_{\text{aragonite}}$ ) of  $>4.0$  are “optimal” and  $>3.5$  are “adequate,” whereas  $<3.5$  is only “marginal”; sea temperatures  $>18^{\circ}\text{C}$  are warm enough to facilitate polyp replication, gametogenesis, and skeletogenesis; solar radiation needs to be sufficient to sustain a dense population of zooxanthellae with a high production of photosynthate. For these reasons, corals are rare and reefs are absent at latitudes  $>35^{\circ}$  north or south of the equator (Veron, 1995); these latitude’s low sun angles, short winter day lengths, low temperatures, and low aragonite saturation (Figure 1) all militate against vigorous coral growth. The geographic or depth limit beyond which coral growth is vigorous enough for reef growth has been termed the “Darwin Point” (Grigg, 1982).

## Chemistry

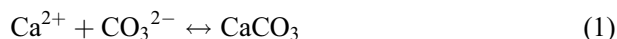
A location’s position on the “optimal to marginal” spectrum of Guinotte et al. (2003) reflects the ease or difficulty



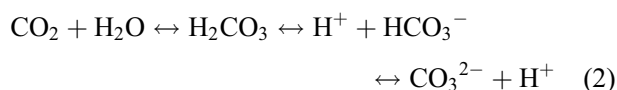


**Coral: Environmental Controls on Growth, Figure 1** Global patterns of latitude-correlated environmental controls on coral growth: light, temperature, and carbonate chemistry. Coral reefs are mostly confined to between 35°N and 35°S of the equator and corals between 40°N and 40°S. *Pie diagrams* indicate (in white) the proportion of each year that daily insolation at the sea surface exceeds 200 Einstein per square metre per day (Source: from [Figure 2a](#), after Beer, 1997). The *broken line* indicates position of 18°C sea-surface temperature isotherm in mid-winter (i.e., January average in northern hemisphere; July average in southern hemisphere. Source: Reynolds and Smith, 1995). *Gray shading* indicates northern and southern limits of "adequate" aragonite saturation for coral calcification (source Kleypas et al., 2001).

with which calcium carbonate is deposited by reef plants and animals. It depends in large part on  $\Omega_{\text{aragonite}}$ , the degree to which the sea water is saturated with the ionic precursors of aragonite calcium carbonate – the form comprising the skeletons of reef-building corals:



There is ample  $\text{Ca}^{2+}$  for calcification in all the world's sea waters (Gattuso et al., 1999). (Indeed, excess  $\text{Ca}^{2+}$  is toxic to cellular processes, and biogenic calcification, now the keystone process for coral reef existence, is believed to have initially evolved in the Cambrian as a  $\text{Ca}^{2+}$  detoxification mechanism; Brennan et al., 2004; Kleypas and Langdon, 2006). But the amount of carbonate ( $\text{CO}_3^{2-}$ ) available can become limiting, because it is very easily converted to the unusable bicarbonate ( $\text{HCO}_3^-$ ) in the presence of  $\text{H}^+$  ions: (the lower the pH, the less the  $\text{CO}_3^{2-}$ ).  $\text{H}^+$  ions are evolved when  $\text{CO}_2$  dissolves in water, forming carbonic acid ( $\text{H}_2\text{CO}_3$ ), which then dissociates:



More  $\text{CO}_2$  in solution (Equation 2) means more  $\text{H}^+$  is evolved and more  $\text{CO}_3^{2-}$  is robbed from the feedstock (Equation 1) that could otherwise have been joined with  $\text{Ca}^{2+}$  in the skeleton of a reef-building organism. Temperature also affects the solubility of  $\text{CO}_2$  (and all other gases) in seawater: the warm waters of the tropics absorb less  $\text{CO}_2$  than cool temperate waters, and therefore, less  $\text{CO}_3^{2-}$  is robbed from calcification in the tropics, historically to the great advantage of corals.

### Solar radiation

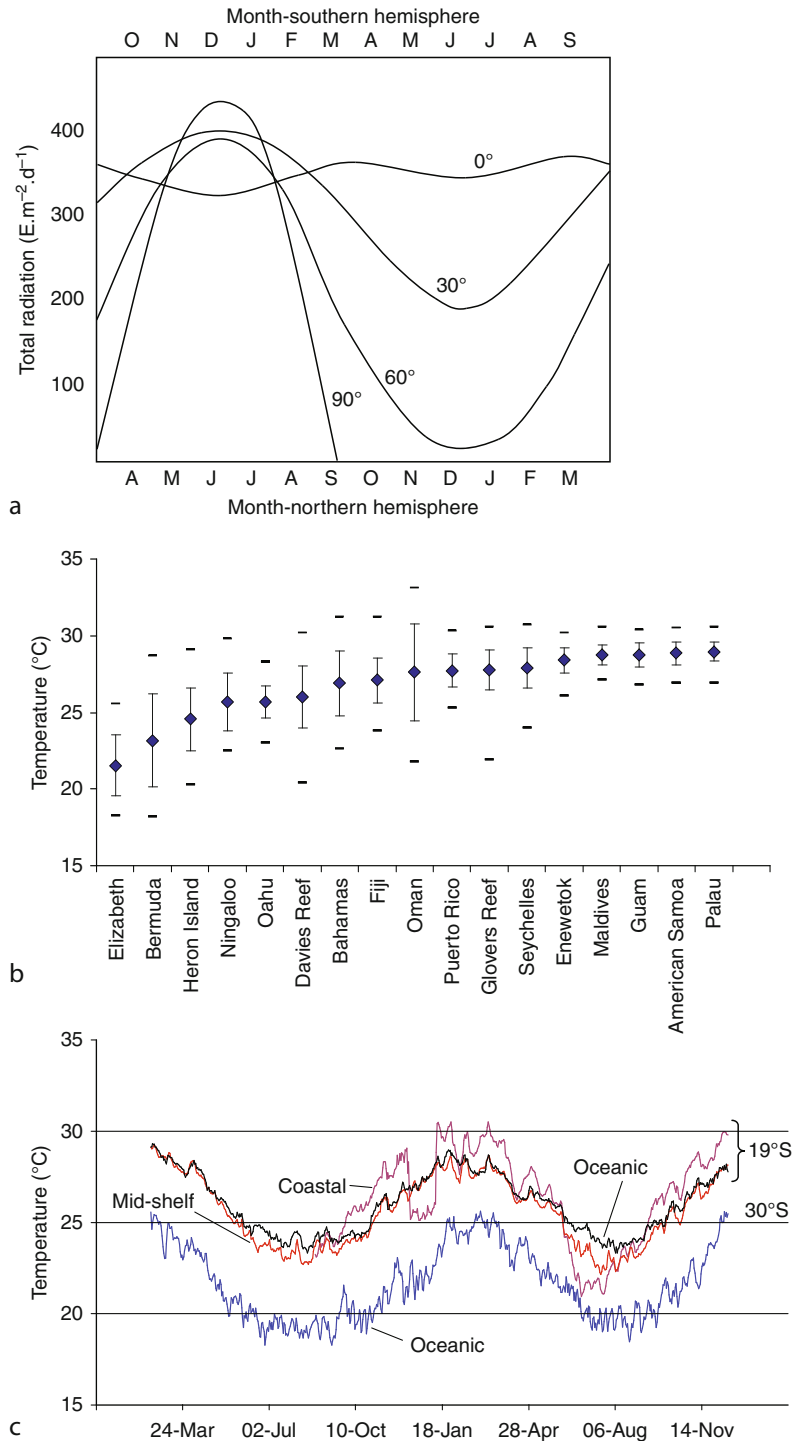
Solar radiation is a primary environmental driver of production on coral reefs, both organic matter (tissues of plants and animals) and inorganic matter (skeletons), the latter at rates of up to tens of tonnes of calcium carbonate per hectare per year (Kinsey, 1983). The part of the solar radiation spectrum that drives this production is referred to as photosynthetically active radiation (PAR – wave lengths 400–700 nm). Quanta in this range are absorbed by the photosynthetic systems of the zooxanthellae, driving their production of the energy-rich “photosynthate” (glycerol and glucose). Around 95% of the photosynthate is translocated from the zooxanthellae to the cells of the coral host and used throughout the coral colony to build coral tissues, gametes, and aragonite. Calcification occurs at its maximum rate for 4 h around local solar noon (Chalker, 1983), during which time the irradiance of shallow corals with PAR is “saturating” with respect to the ability of the photo systems within the zooxanthellae to use it. The excess irradiance elicits “photoinhibition” in the coral, viz, a reduced photosynthetic efficiency, capacity, or both, compared to the performance at optimal levels of irradiance (Winters et al., 2003). At the high latitude limits of coral distribution, vigorous growth of

“phototrophic” corals (those for which photosynthesis is the primary energy source) is precluded by the meager annual quota of PAR both at the water surface (due to short winter day lengths and low sun angles – Figures 1 and 2a) and at depth (due to reflection and absorption – Baker and Smith, 1982).

### Temperature

Corals are “poikilothermic” organisms (they cannot regulate their temperature and must operate at the ambient temperature). Diverse coral communities and reefs occur in waters with sea temperatures in the range 18–28°C (Figure 2b). Throughout this range, there are suites of corals for which local temperatures are conducive to tissue growth, skeleton growth, and reproduction: the same coral species can host different types (Clades) of zooxanthellae to suit its particular environmental setting. For example, in the tropics, the world's most widely distributed zooxanthellate coral species *Plesiastrea versipora* (Veron, 2000) hosts zooxanthellae that are predominantly of the ubiquitous Clade C (Rodriguez-Lanetty et al., 2001), a highly efficient photosynthesizer (Cantin et al., 2009) that confers a fast growth rate on the many coral species in which it occurs. However, to survive in temperate waters, *P. versipora* hosts predominantly zooxanthellae of Clade B, which can function and survive at lower temperatures than Clade C (Howe and Marshall, 2002). Likewise, some coral species occupy warmer habitats by hosting warm-adapted zooxanthellae, in this case, predominantly Clade D (Berkelmans and van Oppen, 2006; Cantin et al., 2009). Compared to Clade C, however, the tolerance to marginal temperatures in both cases comes at the cost of a reduced growth rate (Howe and Marshall, 2002; Little et al., 2004). This trade-off has permitted corals to spread widely along the latitude-correlated attenuation of the parameters that govern coral growth: viz, temperature, aragonite saturation, and light. Whereas the zooxanthella complement of adult corals is typically dominated by a single clade, juveniles in some coral species host a mixture of clades (Gómez-Cabrera et al., 2008). The extent to which the identity of the clade dominant in the adult represents a form of selection to the type most suited to the individual coral's micro-environment has yet to be established (Gómez-Cabrera et al., 2008).

With normal local seasonal changes in temperature (~5–7°C – Figure 2c), the coral's metabolism is channeled variously into growth and replication of polyps, gametogenesis, skeletogenesis, and manufacture of stored energy reserves (Harriott, 1993). However, a few days of temperatures outside a particular reef's normal variability can be stressful and sometimes lethal for corals, be they abnormally high temperatures or abnormally low. Temperatures only 1–2°C above its normal summer maximum or below its normal winter minimum can cause coral bleaching (Brown, 1997): hot water bleaching (Goreau and Hayes, 1994) or cold water bleaching (Muscatine et al., 1991). In both cases, the anomalous



**Coral: Environmental Controls on Growth, Figure 2** Global and regional variability in reef environments. (a) Seasonal variability in daily irradiance at the sea surface at latitudes indicated (modified from an original figure by Beer, 1997). (b) Annual temperature variation in sea-surface temperatures at a global selection of coral reefs. Source: Elizabeth Reef – Data Centre, Australian Institute of Marine Science, <http://www.aims.gov.au/docs/data-centre/seatemperatures.html>. Remainder: NOAA “Coral ReefWatch” [http://coralreefwatch.noaa.gov/satellite/current/sst\\_series\\_24reefs.html](http://coralreefwatch.noaa.gov/satellite/current/sst_series_24reefs.html). (c) Seasonal variability in sea-surface temperature at reefs at two latitudes on the east coast of Australia. Coastal temperatures are most volatile, and oceanic temperatures are the least.



temperatures can cause expulsion of zooxanthellae, loss of photosynthetic pigments, and subsequent decline of physiological performance, including calcification (Porter et al., 1989), and in severe cases, it can cause death of the coral (Loya et al., 2001). Beyond the latitudinal margins of coral and reef distribution, cold water events, superimposed on low light and aragonite saturation, are sufficiently frequent to cease to be anomalies and to be considered part of a normal seasonal variability that excludes phototrophic corals from establishing and growing, even on suitable substrata. For that reason, the corals on deep cold water reefs lack zooxanthellae, rely entirely on particulate food, and grow very slowly (Roberts et al., 2006).

### Environmental variability within regions

Within the broad bounds set by water chemistry, temperature, and solar radiation (see above), environmental factors affecting coral growth also vary greatly over scales of kilometers to tens of kilometers: nature and depth of the substratum, temperature (Figure 2c), wave climate, salinity, water clarity, nutritional properties of that water, and sedimentation regime. Clear waters have traditionally been considered “optimal” for coral growth, and naturally turbid water reefs “marginal,” but for the purposes of the present account, they are viewed as “just different” (Perry and Larcombe, 2003).

### Hydrodynamics, light, and sediments

Either too little or too much water motion can limit coral growth and survival. Whereas in moderation, water motion facilitates gas and nutrient exchange through the coral’s surface tissues (Atkinson and Bilger, 1992), strong waves and currents cause physical destruction (see *Hydrodynamics in Coral Reef Systems; Tropical Cyclone/Hurricane*), and insufficient flow limits gas and nutrient exchange to the detriment of coral health and survival. Too little flow, which exposes corals to potentially fatal physiological stress, can occur over large areas of the ocean in doldrum conditions. Corals in enclosed reef flats and lagoons are particularly vulnerable to high temperatures, flat glassy waters, and prolonged periods of calm weather. Low- or no-flow conditions thicken the diffusive boundary layer around corals, reduce gas exchange, and make it hypoxic, inducing anaerobiosis in the coral. Moreover, intense light beams condensed by surface ripples can exacerbate the stress caused by high temperatures and low flow, causing corals to bleach at such times (Nakamura and van Woesik, 2001).

Within those habitats where water is in motion, hydrodynamic variables (wave climate, currents, and residence time – see *Hydrodynamics in Coral Reef Systems*) are important determinants of where corals can grow and what morphological form they adopt. In oceanic settings, reefs and islands offer a broad range of environments for corals. Shallow reefs that are exposed to the full force of ocean swells and breaking waves do not necessarily support

significant coral growth. On the outer Great Barrier Reef, for example, corals do build physically robust, wave-resistant structures in the surf break area (Done, 1982). But adjacent areas of the reef are often occupied by coral assemblages consisting of mainly small, short-lived corals, whose longevity is severely limited by recurrent breakage, scour, and abrasion. The latter structure and ephemeral dynamics are comparable to those described for some shallow reef slopes on Oahu, Hawaii, where the turnover of corals is so great that the coral veneer is rarely thicker than a single living colony (Grigg, 1998). The contrast of wave-beaten reefs with those of highly enclosed, shallow reef lagoons and embayments is striking. These latter habitats are often occupied by dense and extensive populations of corals whose shapes, sizes (often large), and longevity (often very great) are extremely variable from place to place, their specific composition dictated by the composition of the regional species pool, founder events, and environmental factors other than waves, such as light, sediments, and currents.

On continental shelves, there are greater complexities of environmental pattern and process, as exemplified in the Great Barrier Reef (GBR), whose 2,900 reefs are distributed across a seafloor that slopes from coastal beaches and headlands to a depth of ~80m at the shelf edge 50–100 km offshore. On most days of the year, big, long period waves generated by distant meteorological drivers surge through interreef passages and break on the outermost reefs. They dissipate strong hydrodynamic forces in the reef’s surf zones and across their tops (Hearn, 1999), and, in conjunction with tidal flows, set up powerful turbulent jets and eddies around their flanks (Wolanski and Hamner, 1988). Depending on reef size, shape, orientation, weather, and state of the tide, different places along the leeward sides of these outer reefs may be completely calm, or they may be impacted by waves from the opposite direction, generated by local winds. These wind waves, which are of smaller wave height and shorter period than the ocean swells, intersect and combine with those oceanic swells that penetrate to behind the outer reefs and then lose height, velocity, and power as they are intercepted by mid-shelf reefs. As they travel into shallow coastal waters, further energy is lost to bottom friction, coarse sediments are rolled along the bottom, and fine sediments are resuspended and mixed through the water column, making it turbid (suspended sediment concentrations of 10–100 mg l<sup>-1</sup> – Larcombe and Carter, 2004). When the winds subside and tides slacken, the coastal waters clear, as suspended sediments fall to the bottom.

### Nutrients

Corals need fixed nitrogen (NH<sup>4+</sup>, NO<sup>2-</sup>, NO<sup>3-</sup>) and phosphate (PO<sub>4</sub><sup>3-</sup>) to synthesize proteins and nuclear material for cell maintenance, growth, and reproduction, and they are well adapted to exploit them in the low concentrations of oligotrophic surface waters in the oceans. However, excess nutrients are detrimental to coral growth

for a number of reasons (Hallock, 2001; Fabricius, 2005): they can limit PAR reaching corals by promoting phytoplankton blooms that reduce water transparency; they can promote the growth of the algal competitors of corals (especially when grazing organisms are scarce); they can promote bioerosion and excessive phosphate can inhibit formation of  $\text{CaCO}_3$  crystals. Excessive N also promotes the proliferation of zooxanthellae within corals (Dubinsky and Jokiel, 1994), which appears to detrimentally affect growth (Lesser et al., 1994) and to increase the coral's sensitivity to elevated temperatures, and thus the likelihood of lethal bleaching (Wooldridge, 2009).

There are four sources of nutrients to coastal waters: rivers, terrestrial dust, rainfall, and upwelled ocean waters. Dissolved concentrations of key nutrient elements required by corals and their zooxanthellae are usually extremely low on coral reefs due to low input rates, huge dilutions, and uptake by phytoplankton and pelagic bacteria (Furnas et al., 2004). Much of the terrigenous nutrient that flows into coastal waters is rapidly incorporated in phytoplankton–zooplankton–fish food webs (Furnas et al., 2004), to the potential benefit of coastal shrimp and fin-fish fisheries. However, the food web itself can deliver excess nutrients into the waters bathing corals: the feeding detritus and fecal pellets generated by this food web are fed on by microbes, which in turn release dissolved nutrients, with the potential to affect corals detrimentally as described above.

### Microenvironment controls on coral growth

A coral's microenvironment consists of (1) *resources* (that it must receive at adequate rates and continuity of supply); (2) *sublethal stresses* (sometimes called “press disturbances” – Connell, 1997), which reduce its capacity to use resources efficiently (e.g., suboptimal temperatures or salinities; low-level pollutants); and (3) *extreme events* (sometimes called “pulse disturbances” – Connell op. cit.), which may kill, injure, or dislodge it during events of short duration (hours to weeks). Extreme natural events, which have characteristic return intervals generally measured in years to decades, include anomalies (high or low) of temperature or salinity, exposure to air (Figure 3), predators (see *Acanthaster planci*), disease, and destructive waves (see *Tsunami*; *Tropical Cyclone/Hurricane*).

On any given reef, corals distribute themselves across ambient environments that are extremely wide ranging, from bright wave-beaten surf zones, across shallow reef tops, and down reef slopes to deep placid twilight zones. Two levels of diversity in the assemblage allow it to occupy such a broad range of environments: the number of available coral species and the plasticity within each species (capacity to adopt a modified form of their basic growth plan). In highly plastic species (the majority), a larva or a fragment will adopt a particular adult growth form that is suited to the precise location in which it happens to settle (e.g., *Acropora humilis*, which adopts



**Corals: Environmental Controls on Growth, Figure 3** Exposure to air – the ultimate environmental limit to the upper limit of coral growth. Corals (several species in the genus *Acropora*) exposed to the air during an extreme low tide event. Wheeler Reef, Great Barrier Reef, July 1986.

a robust form in the surf zone and a lighter structure in deeper waters: *Acropora palmata*, which orients its branches with the waves in the strongest waves, across them in moderate waves, and indifferently to them in calm areas). In species with only one growth form option, the larva or fragment will likely survive only in a single narrowly confined habitat [e.g., *Acropora pyramidalis*, *A. nana* (robust and delicate corals, respectively, found only in surf zones); *Pachyseris robusta*; *Pachyseris speciosa* – encrusting plates, found only in calm waters].

Corals most often attain their highest abundance, percentage cover, and diversity on reef margins (Kinsey, 1983; Macintyre, 2007), i.e., in horizontal zones usually not more than 30-m wide along the edges of intertidal reef flats; on reef slopes, particularly in the upper 20 m and on the margins of lagoonal patch reefs. One reason that corals are abundant in such areas is because these are the habitats that are first encountered by coral larvae carried to the reef by currents. Once established, these corals have first use of waters that flow or break onto the reef. Most aspects of the environment of shallow margins are optimal for coral growth: influx of solar-radiation is nonlimiting; on-flowing water is most saturated in the precursors of coral growth (see Section Chemistry) and richest in the

particulate matter on which corals feed (especially zooplankton); and temperature is the same as the adjacent sea (Figure 2c).

As water crosses the shallow reef, key properties are changed by its interaction with the shallow reef and its biota (see *Hydrodynamics in Coral Reef Systems*). For example, the margin-inhabiting corals (and other calcifying organisms) extract calcium carbonate precursors and nutrients from the water, reducing the levels available to corals “down-stream” (i.e., toward the middle of the reef flat). Calcification by a community reduces the water column’s total carbon and alkalinity, resulting in a decrease of  $\text{CO}_3^{2-}$  (reviewed in Nakamura and Nakamori, 2007). When different reef communities are aligned across a reef from their wave-exposed to their sheltered side, their exchanges with the passing water set up seaward to leeward gradients in pH, total carbon and total alkalinity. In effect, the upstream communities strip  $\text{CO}_3^{2-}$  from the water, limiting its supply to sheltered backwaters, making calcification there impossible. Where corals do grow in such back reef areas, it indicates that seawater with the correct pH, total carbon, total alkalinity, and composition of carbonate species is reaching that place via routes other than a transit across a productive reef flat (e.g., refraction around reef flanks or through broad channels).

Shallow water on reef flats can be easily heated beyond the range preferred or tolerated by corals. This greater temperature volatility is amplified by low-tide ponding and other restrictions on its rate of flushing caused by prior growth of the reef itself (Macintyre, 2007). Where back-reef waters are highly impounded, they can become sinks for rainfall and land-runoff, and for inorganic and organic detritus from the reef upstream, with regimes of temperature, oxygenation, salinity, and turbidity that are inimical for coral growth. Where, by contrast, back-reef habitats are well flushed with ocean waters, corals can grow profusely on sandy lagoon floors and on the margins of back-reef pinnacles and walls.

Solar radiation reaching a coral varies in both space and time, and the key drivers of variability have been reviewed by Anthony et al. (2004): (1) seasonal pattern of daily surface irradiance; (2) variations in clouds; (3) transmittance through the water column, which depends on the optical properties of the water (Baker and Smith, 1982), most notably turbidity; and (4) tides, whose daily and seasonal cycles always affect the depth of the water column and in some circumstances influence turbidity. In a clear oceanic setting, a gradual depth-attenuation of PAR allows corals that are primarily phototrophic to grow to depths as much as 100 m. By contrast, in turbid coastal waters, dissolved and suspended matter attenuates PAR to below useful levels at <20 m. However, corals that gain most of their food by feeding (i.e., heterotrophic corals) can thrive in low light settings, be it deep on a clear water reef or much shallower on turbid water reefs. In both cases, something else may set the lower depth limit to coral distribution; a steep unstable talus in the oceanic reef; a flat muddy sea floor in the coastal reef.

## Coral growth

### From primary polyp to coral colony

There are approximately 700 species of Scleractinian corals globally (Veron, 2000). Based on their adult shapes, they can be divided into six broad “growth-form” categories (Veron, 1996): *massive* (similar in all dimensions); *columnar* (forming columns); *encrusting* (adhering to the substrate); *branching* (arborescent or tree-like to digitate or finger-like); *foliaceous* (leaf-like); and *laminar* (plate-like). There is considerable variability in the detailed morphology among and within species: for example, massive corals may be taller or squatter; columns may be thick or thin, long or club-like; encrustations may be thick or thin; and branches may have different shapes, thicknesses, densities, taper and departure angles of secondary and tertiary branches, which may or may not fuse. A major contributor to this growth form variability is the local environmental setting, which has a comparable effect to that of the coral’s genetic makeup (Veron, 1996) in transformation of the microscopic primary polyp into a flat, fingernail-sized spat, and thence up and out into a particular locally adapted variant of the basic growth form.

The primary polyp develops from a soft-bodied planula larva (see below) that transforms itself into a single soft-bodied polyp within hours of settlement (Hirose et al., 2008), when it glues itself onto something solid (e.g., mollusc shell, dead coral in situ, rubble, rock, or reef framework). The “glue” becomes a perforated shallow calcium carbonate saucer with radial costae (spiky ridges) on top that support the polyp’s tissues. This single act of transformation from soft-bodied larva to skeleton-secreting “zooid” (polyp + skeleton) marks the commencement of a period occupancy that may continue for centuries and produce a colony meters high and meters across.

The adult coral colony that eventually develops has one of the basic growth forms listed above. All except “solitary” corals (in which the original zooid just continues to grow, reaching the size of a desert plate or hefty fruit bowl in a matter of a few years) undergo a process of modular growth. Modular growth occurs through vegetative replication (e.g., budding or expansion, and subdivision) of the original zooid and all of its descendants – Rosen, 1986; Kim and Lasker, 1998). While the basic growth forms are constrained genetically, actual colony morphologies adopted by a particular colony of a particular species in a particular place will in large measure be a phenotypic response to its microenvironment: viz, the regimes of chemistry, nutrition, temperature, and light and wave energy that are incident upon it.

Some large coral colonies originate from an unattached fragment, essentially a small version of the adult colonies, for which the environmental milieu is qualitatively similar to that of the adult. However, being unattached means it can be dislodged, projected, or rolled by strong currents (Fox et al., 2003). In wave-swept reef habitats, where oscillating flows make such motion a daily occurrence, it



usually kills the remaining polyps and the fragment becomes rubble. In habitats where a fragment is immobilized by lodgment in a crevice or falling into a sheltered place, or is inverted only at intervals of weeks to months at most, the living veneer of polyps survives and deposits an increasing mass and volume of skeleton. In shallow flat habitats with reversing currents, a ball-like *corallith* with live polyps on all sides may develop (Glynn, 1974). But in most viable habitats, the fragment will produce skeletal processes that attach it to adjacent stable substratum and prevent further rolling. Once attached, the environmental needs and vulnerabilities are the same as for other attached corals of comparable size.

### Modes of nutrition and coral growth forms

Corals need both large supplies of energy-rich compounds and small amounts of nutrients (N, P) for their growth (tissue and skeleton) and reproduction. Modes of nutrition of corals can be arranged along a spectrum of relative reliance on ingested food as a primary source of energy-rich compounds (Hallock, 2001). In “phototrophic” corals, it is small (but necessary for intake of N and P), and the corals primarily use “photosynthate” (the product of photosynthesis by their symbiotic zooxanthellae). In “heterotrophic” corals, at the other end of the spectrum, there is major reliance on ingested food (zooplankton, organic detritus, and dissolved organic matter). In the middle are “mixotrophic” corals, which use both sources more equally.

Corals build exoskeletons in shapes that facilitate their particular mode of resource use, i.e., adequate interception of solar radiation and particulate food and the water-borne precursors for calcification; use of the moving water to remove the waste products of metabolism. In calm, clear, shallow waters, there is so much light that virtually any shape will be effective in harvesting sufficient PAR. Indeed, these phototrophic corals have to expend energy producing compounds to protect themselves against damaging excess irradiation. However, in wave breaking and surging zones, the range of coral shapes is more limited. These include encrusting forms and/or small colonies of species that adopt a top-heavy form in calmer waters and streamlined and elongated variants of growth forms that are more radially symmetrical in calm waters: e.g., *Acropora palmata* in the Atlantic and several *Acropora* groups in the Indo-Pacific: “*robusta*,” “*humilis*,” “*nasuta*,” and “*palifera*.” Only those shapes that can resist dislodgement by normal fair-weather waves can survive for long, and even they will eventually reach a size where their dislodgement is likely (Massel and Done, 1993; Madin and Connelly, 2006; see also *Tropical Cyclone/Hurricane*).

### Depth and light

In deep or turbid water, phototrophic corals often adopt horizontal growth forms to maximize the interception of PAR. However, in places where this exposes them to

a rain of sediments falling out of the water column, corals survive by adopting shapes that shed sediments passively or with minimal energy expenditure by the polyps: low convex profiles from which gentle water motion can easily entrain sediment particles; dense networks of flattened branches, perforated with gaps through which sediments can drop and vases whose interaction with the currents sets up a vortex that lifts accumulated sediments clear (Reigl et al., 1996). In some species, notably in the genera *Pocillopora* and *Acropora*, colonies in very sheltered habitats have thinner and more open branches than shallower colonies (Veron, 1995; Wallace, 1999), thereby maximizing extension without investing unnecessarily in a strong skeleton.

The PAR dose reaching corals down a reef slope has been attenuated by absorption and scattering as it passes down through the water column (Baker and Smith, 1982). Deeper phototrophic corals compensate for reduced PAR by elevating zooxanthellae densities, chlorophyll content per zooxanthella, or both. These changes cause them to appear more darkly colored than shallow water corals. In clear waters, corals as deep as several tens of meters can remain saturated and function normally (Chalker, 1983).

In turbid waters, this depth may be only a few meters. There, the day-to-day and week-to-week variation in irradiation a few meters down the slope can, due to frequent resuspension of mud from the adjacent shallow sea floor, be more than an order of magnitude greater than it is at the surface and at equivalent depths in offshore, clear-water benthic habitats (Anthony, 2000; Anthony et al., 2004). Corals on slopes of turbid-water reefs may thus alternate between periods of light deficiency and light excess. Phototrophic corals are therefore confined to the relatively well-lit shallower parts of such reefs, whereas deeper, darker, and muddier parts of these reefs are populated by corals with specific adaptations for those conditions. In very dark (deep or very turbid) waters, only mixotrophic or heterotrophic corals can survive (Anthony, 2000). These corals largely replace the now minimal zooxanthellae-derived photosynthate as the primary food source with dissolved organic matter (saprohagy) or particulate organic matter (detritus and/or zooplankton) (Anthony et al., 2004). In deep (50–4,000 m), dark cold-water coral reefs (4–12°C), approximately ten species of scleractinian corals have been discovered, all completely lacking zooxanthellae (Roberts et al., 2006). They rely entirely on food transported from surface waters to the sea floor, frequently in sites with food supply enhanced by locally accelerated currents.

Ultraviolet radiation (UVR – 390–400 nm) is potentially damaging to corals. However, a number of things protect corals from UVR damage. First, is depth itself: shorter wavelengths are scattered by particles and absorbed by water molecules and dissolved organic compounds more readily than PAR wavelengths (Baker and Smith, 1982). As a result, UVR attenuates to near zero within a few meters at most, and because of the extreme

scattering, they irradiate the corals only weakly. Second, shallow corals manufacture sunscreens [mycosporine-like amino acids (MAAs) – Dunlap and Shick, 1998] that shield their tissues from any ambient UV that does reach them. These compounds are especially important for those corals that are periodically left emerged at extreme low tides (Figure 3) and thereby exposed to direct sunlight. Some of the MAAs produced by the corals occurs in mucus that is secreted by emergent corals and protects them from dehydration.

### Environmental controls on coral's presettlement stage

The environmental milieu of the coral's presettlement stage is quite different to that of adult corals. Corals develop by two main methods (Harrison and Wallace, 1994; see also *Corals: Biology, Skeletal Deposition, and Reef-Building*): asexually (from the fragments of an existing colony that become separated by budding or breakage from a parent colony – see Section Coral growth) and sexually (from fertilized eggs that grow into pelagic larvae that swim or are carried by currents to their place of settlement). Pelagic coral larvae are released into the water by sexually mature corals (usually >3–5 years old) that produce sperm and eggs. Depending on species, the production of the larvae follows one of the two pathways (1) broadcast spawning or (2) brooding. In broadcast spawning, gravid polyps expel eggs and sperm into the water column during a mass spawning event whose timing is synchronized to lunar cycles. Fertilization takes place in the water column, and the drifting fertilized egg transforms itself into a planula larva over a period of several days (Hirose et al., 2008). During its days in the currents, the metamorphosis from egg to larva is fueled by lipids originating from the egg. Once it has developed its simple gut (~4 days), it can feed on phytoplankton and detritus and presumably does so if it is nowhere near a suitable place to settle (Richmond, 1987). However, at this stage it is competent to settle (Hirose et al., 2008), and it tends to do so quickly when deprived of food in the laboratory (Hirose et al., 2008). When food is supplied, individuals of some species can settle within 2–3 days (Miller and Mundy, 2003). For those that do not settle so quickly, there can be major mortality within the first few days, but survival of others in the water column upwards of 100 days (Graham et al., 2008). During this time they are potentially exposed to environmental hazards such as hyposaline areas, excessively muddy areas, or very clear areas where they may become exposed to damaging doses of UVB radiation (Gleason and Wellington, 1995). In open waters between reefs, they will likely be aggregated into fronts generated by the current's interaction with headlands, islands, and reefs; this aggregation on one hand attract predatory fishes or shrimps, but on the other, take cohorts of competent larvae to potential settlement sites (Wolanski and Hamner, 1988). The broadcast-spawning strategy described above favors colonization of widely dispersed

reef substrata and hence the maintenance and/or restoration of those area's reef-building potential (see *Coral Reef, Definition*).

The brooding strategy, by contrast, leads to localized settlement that favors persistence of the local population and local reef-building. In brooding coral species, fertilization takes place within the polyps of the parent colony and so does metamorphosis into the planula larva (Harrison and Wallace, 1994). When expelled several days after fertilization, they are strong swimmers, zooxanthellae bearing, and competent to attach to the reef within minutes to hours of release: they avoid the hazards of days to weeks in the water column that are faced by broadcast pelagic larvae. Brooded larvae have much higher likelihood of finding a suitable settlement place, in this case, close to one that has been tried and tested by the parent colony.

When broadcast larvae are swept over a reef from the sea on a flooding tide, they face the environmental hazard of "the wall of mouths" (Hamner et al., 1988) belonging to coral polyps (Fabricius and Metzner, 2004) and schools of planktivorous fishes that ride the surge along reef edges (Hamner et al., 2007). Those that survive will then receive environmental cues to a potential place for settlement. A hydrodynamic cue alone (Abelson and Denny, 1997) may attract them to within centimeters of solid substrata. Their choice of specific microcrevices may then be guided by chemical cues emitted by coralline algae and microbial films coating the substratum (Harrington et al., 2004). Abelson and Denny (1997) suggest that when hydrodynamic forces are higher than the larva's swimming capacity (as may often be the case in wave-swept reef environments), final site selection may be due to desertion of unfavorable sites rather than exploration and active selection of an appropriate site. For many species it is only after the coral larvae has settled and transformed itself into a rudimentary polyp that it acquires zooxanthellae that multiply within its tissues (Hirose et al., 2008) and contribute to the nutrition of their host.

Reef environments present a wide range of colonizable substrata for the establishment of corals that could occupy that place for decades or even centuries. In wave-swept parts of the reef, the substratum to which a coral attaches is usually big and heavy enough to stay in place against normal hydraulic forces generated by waves (e.g., solid framework and heavy rubble). In sheltered parts of the reef, smaller rubble sizes (coral shingle and mollusc shells) can be colonized by coral larvae, and even sand and mud can be colonized by coral fragments of some species.

### Global climate change: implications for coral growth

The net effect of global warming and increases in atmospheric CO<sub>2</sub> per se are detrimental to the biological calcification process (Feely et al., 2004; Hoegh-Guldberg et al., 2007; Guinotte and Fabry, 2008). There is so much more

atmospheric CO<sub>2</sub> at the ocean–atmosphere interface today (385 ppm in 2010) compared to preindustrial times (280 ppm) that much more goes into solution, despite the marginal solubility loss caused by increased sea temperature (Sabine et al., 2004). These authors report that if CO<sub>2</sub> reaches double preindustrial levels (560 ppm), there will be a 30% decrease in carbonate ion concentration and a 60% increase in hydrogen ion concentration. There are likely to be differences among calcifiers in their responses to decreasing carbonate ion concentrations, reflecting differences in their carbonate mineralogy and local environmental parameters such as temperature, light, and available nutrients and in the mechanism of biomineralization (Feely et al., 2004). A review by Guinotte and Fabry (2008) suggests that this would cause a 20–60% reduction of calcification rates in tropical reef-building corals, manifest in the skeleton in its two measurable parameters: rate of linear extension (cm day<sup>-1</sup>) and density (g cm<sup>-3</sup>) (Barnes and Chalker, 1990; Lough and Barnes, 2000). Any loss of density would cause a decrease in strength and greater vulnerability to storms in corals on the reef (Massel, 1999). A reduction in linear extension rate would mean that individual colonies would take longer to reach size-related thresholds, such as sexual maturity (Albright et al., 2008), escape from overgrowth by other benthos, or vulnerability to dislodgment by storm waves (Massel and Done, 1993; Madin and Connelly, 2006). Most recent field studies have shown a reduction in linear extension and density coincident with rising temperature and atmospheric pCO<sub>2</sub> over recent decades (Cooper et al., 2008; De'ath et al., 2009; Tanzil et al., 2009). A number of studies (noted in Albright et al., 2008) have reported that reduced calcium carbonate saturation has no negative effect on physiological processes other than calcification (viz, tissue growth and photosynthesis) and indeed may even augment them. Paradoxically, any decline in reef-wide calcification caused by atmospheric CO<sub>2</sub> will reduce aqueous CO<sub>2</sub> emanating from the reef itself. Reefs as a whole, including their reef flats and lagoons, tend to be sources of CO<sub>2</sub>, due both to calcification by reef communities and the decomposition of plant matter produced on the reef (Suzuki and Kawahata, 1999).

Anthropogenic climate change may be precipitating the sixth great coral reef extinction in 430 million years (Veron, 2008). Reefs are confined to warm shallow waters that are becoming too hot too often, bleaching and killing coral populations on reefs scattered over vast areas of ocean. As a result, recolonization of damaged areas will be weakened, and even in those places where by chance there is good recolonization, the next heatwave, hurricane, flood, pest outbreak, or disease will cut off recovery of high coral cover before it can be completed. Refuge populations themselves are threatened. For shallow ones, it may simply be a matter of time before they are killed by a heatwave, and for deeper and cooler ones, before they become victims of shallowing of the aragonite saturation zone caused by ocean acidification (Feely et al., 2004). This view of the future – predicated on the assumption

that environmental changes will be too great and are occurring too fast for there to be any effective adaptation in reef organisms (see Chapter *Adaptation*) – raises some key questions about the viability of the processes and circumstances responsible for maintaining modern coral reefs, i.e., environmental controls on coral growth.

## Summary

Coral growth (individuals, populations, and communities) responds to variations in their external environment that are manifest over spatial scales spanning centimeters to degrees of latitude. The specific microenvironment in which a coral settles and in which it may spend anything from years to centuries is determined by vagaries of currents and early survival. Corals and coral reefs exist within a range of local settings within a region (e.g., oceanic vs. continental shelf) and benthic communities and reefs further modify their own environments – dissipation and refraction of waves; ponding of reef-top waters; removal of aragonite precursors and addition of organic and inorganic detritus. As a result, there may be as much variability in the range of microenvironments existing within regions and on individual reefs as there is across much broader geographic areas. This existing variability in microenvironments and the concomitant diversity in species and coral–zooxanthellae partnerships are extremely important for the survival of reefs in a future with global climate change, in which they are faced with rapid changes in environment over all spatial scales.

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## Cross-references

[Acanthaster planci](#)  
[Adaptation](#)  
[Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity](#)  
[Cold-Water Coral Reefs](#)  
[Corals: Biology, Skeletal Deposition, and Reef-Building](#)  
[Hydrodynamics of Coral Reef Systems](#)  
[Tropical Cyclone/Hurricane](#)  
[Tsunami](#)  
[Waves and Wave-Driven Currents](#)

## CORE PLUGS

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### Definition

Many massive corals contain annual density bands in their calcium carbonate skeletons, similar to tree rings. Growing at  $\sim 1\text{--}2$  cm/year coral bommies<sup>1</sup> several meters in height can contain several hundred years of continuous coral growth. The annual density bands (visible when slices from coral are X-rayed) provide the chronological control for the extraction of a wealth of high-resolution coral growth and coral paleoclimatic records. These make a substantial contribution to understanding the nature and causes of climate variability and change, in the shallow-water tropical ocean regions, prior to the advent of extensive observational records and complement similar records obtained from tree rings, ice cores, and documentary sources.

Accessing this information requires a sample from the coral and bigger, older corals will provide data over a longer time span (Figure 1). The preferred sampling technique requires the extraction of a core from the coral colony with a tubular drill rig (Figure 2). The corer cuts through the concentric layers of colony growth and when the core is removed, a hole through the colony is created from the living surface to the base. The living tissue of

the coral only occupies the outer 0.5–1.0 cm of the colony (the layers below are dead but retain their physical structure), so taking a core 90 mm in diameter removes  $\sim 63\text{ cm}^2$  of live coral.

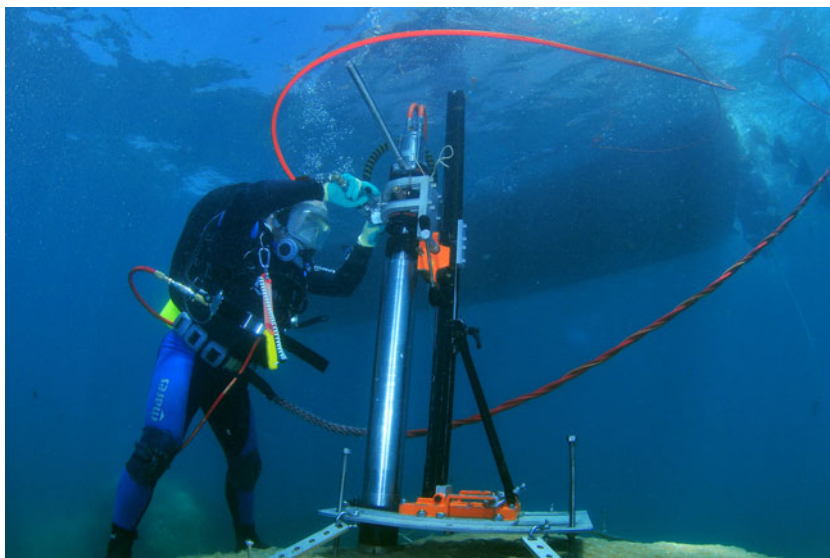
Holes left by coring activities create opportunities for boring organisms to invade a colony and provide a place for sediment to collect and both of these possibilities may cause long term damage to the colony. Many workers seal the core holes with a solid plug to prevent borer access and eliminate sediment collection. Concrete is mostly used to make tapered, cylindrical plugs, slightly larger than the core hole at the big end and slightly smaller at the other end. This taper allows the plug to fit tightly into the hole and remain firmly in place as the coral continues to grow. The plugs are made well before use and soaked in sea water for a month to eliminate soluble components that could damage the coral (Figure 3).

Studies on the Great Barrier Reef (Australia) over a 3 year period have shown that colonies of *Porites* (sp) are not damaged by the plugs and are able to grow over the concrete plugs completely. The rate of regrowth is dependent on the coral species and prevailing environmental conditions. The relief of the plugs is also important; plugs that sit flush with the colony surface are more likely to be grown over, than those that are higher than the surrounding coral structure (Figure 4). In the GBR study which looked at *Porites* regrowth after 50 mm diameter cores were taken, the shortest time taken to completely grow over the concrete plug was  $\sim 30$  months, whilst others were still less than half covered after 36 months. A small



**Core Plugs, Figure 1** Cores taken from massive, long lived corals like this *Porites* sp. can provide data about climatic conditions that pre-date instrumental records.

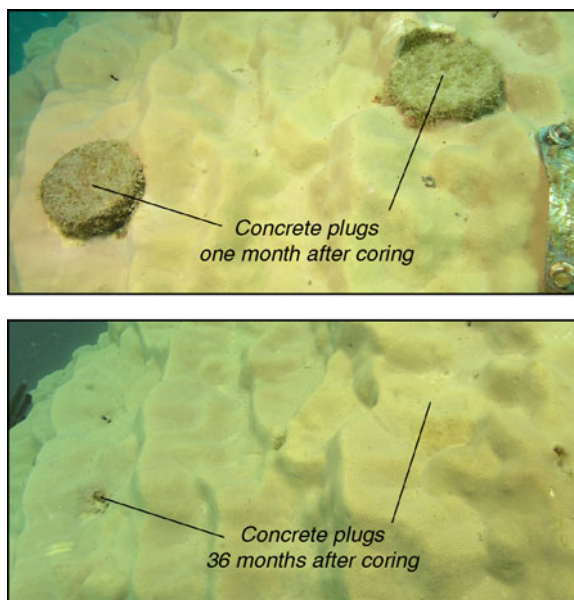




**Core Plugs, Figure 2** Cores are extracted from the colony using a variety of methods, shown here is a powerful hydraulic drill rig clamped in place with the operator about to commence cutting.



**Core Plugs, Figure 3** When the core has been removed, a hole is left in the colony and this is plugged with a tapered, conical, concrete plug. These plugs are pre-washed in sea water to eliminate soluble toxins and are hammered home in level with the natural surface.



**Core Plugs, Figure 4** The *upper portion* of this image shows part of a colony cored and plugged a month before the photo was taken. The *lower portion* of the image shows the same colony 36 months later. The healthy coral has continued growing normally and covered both plugs completely.

number of the colonies showed no growth on the concrete plugs at all.

One of the cored colonies had no plug and acted as a control. This colony not only had apparent damage which could be attributed to the coring activity, but also showed very little of the horizontal growth evident, where plugs were used.

Cores taken from massive long lived corals can provide valuable paleoclimatic information and coral growth histories. The value of these cores must be weighed against the potential risk to the colonies from which the cores are extracted. Sealing the core holes with tapered concrete plugs that have been conditioned by long pre-immersion in sea water reduces the likelihood of long-term damage to cored colonies and in many cases assists the colony to overgrow the damaged area in a relatively short time.

<sup>1</sup>The term “coral bommie” is used in Australia to describe large outcrops of coral often visible from the surface, usually separated from the main reef. In this article, it refers specifically to individual, living colonies of the *Porites* genus as seen in [Figure 1](#).

## Cross-references

[Reef Drilling](#)

# D

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## DALY, REGINALD ALDWORTH (1871–1957)

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Reginald Aldworth Daly (1871–1957) Canadian igneous petrologist, structural geologist, early geophysicist, and originator of the glacial control hypothesis for the origin of modern coral reefs. Educated at Victoria College, Ontario and Harvard University (PhD 1896), where he was a teaching assistant under N.S. Shaler and W.M. Davis. In 1901, he joined the Canadian International Boundary Survey and undertook a monumental survey of structural geology along the 49th Parallel from the Pacific coast through the Cascades and Rocky Mountains into the Great Plains. In 1907, he returned to academic life, first taking a position at Massachusetts Institute of Technology, and then succeeding Davis as Sturgis Hooper Professor at Harvard in 1912, a post he held until his retirement in 1942.

In 1909, he undertook (with T.A. Jaggar, founding Director of the Hawaii Volcano Observatory) early studies of Kilauea volcano, Hawaii and as a member of the Shaler Memorial Expedition to the southern hemisphere (1921–1922), he mapped the volcanic islands of St. Helena and Ascension and studied the Bushveld intrusion in South Africa, the latter leading him to become a supporter of the theory of continental drift. In 1919, on a Carnegie Institution – funded expedition with A.G. Mayor, he mapped the geology of American Samoa. Other interests included carbonate sedimentation and beachrock (with field studies at the Tortugas Marine Laboratory, Dry Tortugas, Florida), turbidity currents and the formation of submarine canyons,

and isostasy and glacial rebound (supported by evidence from raised shorelines in Canada and Fennoscandia). He made a major contribution to coral reef science through the glacial control hypothesis (see [Glacial Control Hypothesis](#)) which drew attention to the importance of Pleistocene variations in sea level and ocean temperature in determining the morphology of modern coral reefs; while many of his inferences on the magnitude of Pleistocene environmental change have been shown to be broadly correct, he overestimated its impact on coral reef morphology.

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### Cross-references

[Beach Rock](#)  
[Davis, William Morris \(1850–1934\)](#)  
[Glacial Control Hypothesis](#)  
[Mayor, Alfred Goldsborough \(1868–1922\)](#)



## DANA, JAMES DWIGHT (1813–1895)

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James Dwight Dana (1813–1895) American geologist, mineralogist, and naturalist. Holder of the Silliman Professorship of Natural History and Geology at Yale College, 1850–1892. Dana was geologist and mineralogist of the United States Exploring Expedition commanded by Charles Wilkes (1838–1842), gaining field experience of volcanoes and coral reefs in Madeira, Kiribati, Tuvalu, the Tuamotu Archipelago, the Society Islands, Samoa, Tonga, Fiji, and the Phoenix and Hawaiian Islands. His expedition reports, published in large volumes with elaborate plates and an atlas, included Zoophytes (1846), Geology (1849), and Crustacea (1852–1855). Dana was the foremost American geologist of his time, writing more than 200 books and published papers, and he held an influential position as editor of the *American Journal of Science*. His highly popular “On Coral Reefs and Islands” published in 1853 (revised as “Corals and Coral Islands” (1872, then 1890)), established coral reefs as a legitimate object of scientific inquiry in North America. One of the key elements in Dana’s writings was his strong support for the Darwinian theory of coral reef development. He tried to refine Darwin’s estimate of the area of the Pacific Ocean characterized by subsidence (as evidenced in Darwin’s (1842) maps of the distribution of barrier reefs and atolls) and came to the remarkable conclusion, prefiguring modern plate tectonic theory, that subsidence had increased across the Pacific Ocean basin from south to north. He recognized the morphological evidence for the sequence of island ages in the Hawaiian Islands and was the first to argue for the paucity of reef development on the eastern sides of the ocean basins as a result of the presence of cool sea surface temperatures. As the “outstanding fluvialist” (Chorley et al., 1964, p. 367) of the mid-nineteenth century, he recognized the fluvial dissection of mid-ocean volcanoes and the relation of valley development and stream density to rainfall patterns on windward and leeward volcanic slopes. His observation that island subsidence would lead to an irregular coastline with large embayments, as commonly seen on volcanic islands lying within barrier reef lagoons, was a powerful proof in favor of the subsidence theory, as recognized by Charles Darwin himself.

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## Cross-references

- [Darwin, Charles \(1809–1882\)](#)  
[Davis, William Morris \(1850–1934\)](#)  
[Subsidence Hypothesis of Reef Development](#)

## DARWIN POINT

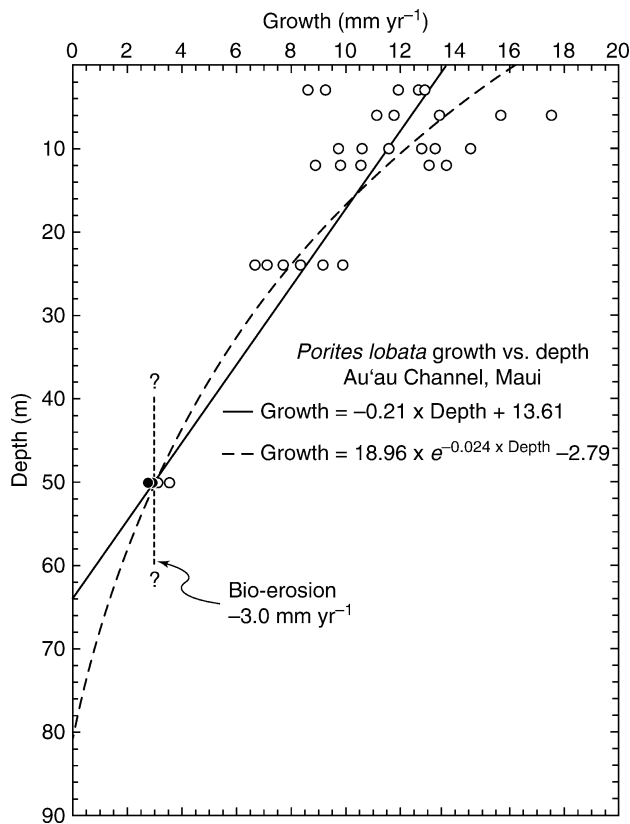
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## Darwin Point

Darwin Points are drowning thresholds for coral reefs and coral islands that have existed in the world oceans since the evolution of reef building corals at the beginning of the Mesozoic Era ~240 Ma (Grigg, in press). A Darwin Point is reached when the net production or vertical accretion rate of CaCO<sub>3</sub> by reef building corals no longer keeps pace with relative sea level. A Darwin Point is exceeded when the reef structure permanently drowns. Drowning occurs when production rates due to coral growth are exceeded by rates of bio-erosion, physical-induced losses, rates of island subsidence, or sea-level rise. During the last transgression, the sea level rose on the order of 130 m (21,000 years B.P. to the present), and many coral reefs in the world drowned. Another classic example where a Darwin Point exists is the northwestern end of the Hawaiian Archipelago (Grigg, 1982) (see [Figure 2](#) in the entry *Hawaiian Emperor Volcanic Chain and Coral Reef History*), beyond which atolls drown and become guyots. Even older and deeper examples are the numerous guyots that dot the northwestern Pacific Ocean that today make up, in part, the Mid-Pacific Mountains (Flood, 1999).

Clearly, there are many causal factors that potentially produce “Darwin Point events,” and there is an abundant literature on the question of why coral reefs fail (drown) (Chave et al., 1972; Hopley, 1982; Grigg and Epp, 1989; Grigg, 2006). In the modern day, perhaps the most common examples of Darwin Points are the vertical depth limits of reef building corals set by light extinction or a combination of factors including light extinction, bio-erosion, temperature stratification, or sedimentation ([Figure 1](#)). Looking at the future and to the possible effects



**Darwin Point, Figure 1** Vertical Darwin Point of the major reef building coral, *Porites lobata*, in the Au'au Channel, Maui, SE Hawaiian Islands (Grigg, 2006).

of Global Climate Change, it also seems plausible that many more coral reefs may fail in the not too distant geological future (Mackenzie, 2003).

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## Cross-references

- [Darwin, Charles \(1809–1882\)](#)  
[General Evolution of Carbonate Reefs](#)  
[Hawaiian Emperor Volcanic Chain and Coral Reef History](#)  
[Sea Level Change and Its Effect on Reef Growth](#)  
[Submerged Reefs](#)  
[Subsidence Hypothesis of Reef Development](#)

## DARWIN, CHARLES (1809–1882)

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*Charles Darwin*. British naturalist, 1809–1882, developed subsidence hypothesis for reef development.

## Introduction

Charles Darwin had a profound effect on the theories of coral reef evolution and the subsequent pattern of reef research. In 1842, after some delay due to his ill health, the first edition of Darwin's *The Structure and Distribution of Coral Reefs* was published. In the introduction of the book, Darwin describes its objectives as “to describe from my own observation and the works of others; the principal kinds of coral reefs, more especially those occurring in the open ocean, and to explain the origin of their peculiar forms” (Darwin, 1842, p. 1).

Darwin provides the reader with an explanation for different types of reefs; “lagoon islands” or “atolls,” “barrier,” or “encircling reefs,” and “fringing,” or “shore reefs” (see [Subsidence Hypothesis of Reef Development](#)), for each of which he dedicates a separate chapter (Darwin, 1842). In the introduction to the book, he also provides a brief overview of his theory of coral reefs, including barrier reefs for which at that time, according to him, there was “scarcely one” (Darwin, 1842, p. 4). Thus, according to Darwin “. . . in both atolls and barrier-reefs, the foundation on which the coral was primarily attached, has subsided; and that during this downward movement, the reefs have grown upwards. This conclusion, it will be further seen, explains most satisfactorily the outline and general form of atolls and barrier – reefs, and likewise certain peculiarities in their structure” (Darwin, 1842, p. 4). (see Chapter [Subsidence Hypothesis of Reef Development](#)).

This work was not the first time Darwin's ideas on coral reefs had been published. In the introduction to the book, Darwin writes that “A brief account” of his ideas on corals was read to the Geological Society of London in May 1837 and subsequently published in the *Proceedings* (Darwin, 1838). His ideas were also published in the third volume of Fitzroy (1839).

## Voyage of the Beagle and Darwin's coral reef theory

Darwin's theory on coral reefs originally formed during the famous voyage of the Beagle (1831–1836), with Robert Fitzroy as Captain/Commander and Surveyor (Fitzroy, 1839). Fitzroy received his "instructions" for the voyage from the "Lords Commissioners of the Admiralty":

"You are hereby required and directed to put to sea, in the vessel you command, so soon as she shall be in every respect ready, and to proceed in her, with all convenient expedition, successively to Madeira or Teneriffe; the Cape de Verde Islands; Fernando Noronha; and the South American station; to perform the operations, and execute the surveys, pointed out in the accompanying memorandum, which has been drawn up under our direction by the Hydrographer of this office; observing and following, in the prosecution of the said surveys, and in your other operations, the directions and suggestions contained in the said memorandum." (Extract from "Instructions" in Fitzroy, 1839, p. 22).

As pointed out by Chancellor (2008 np), coral reefs "...were in fact one of the key scientific objectives of the *Beagle's* orders from the Admiralty." Certainly, the undertaking of coral reef investigations on the voyage were detailed in the "memorandum" accompanying the instructions:

The circularly-formed Coral Islands in the Pacific occasionally afford excellent land-locked harbours, with a sufficient entrance, and would be well adapted to any nice astronomical observations. . . While these are quietly proceeding. . . , a very interesting inquiry might be instituted respecting the formation of these coral reefs.

An exact geological map of the whole island should be constructed, showing its form, the greatest height to which the solid coral has risen, as well as that to which the fragments appear to have been forced. The slope of its sides should be carefully measured in different places, and particularly on the external face, by a series of soundings, at very short distances from each other, and carried out to the greatest possible depths, at times when no tide or current can affect the perpendicularity of the line. A modern and very plausible theory has been put forward, that these wonderful formations, instead of ascending from the bottom of the sea, have been raised from the summits of extinct volcanoes; and therefore the nature of the bottom at each of these soundings should be noted, and every means exerted that ingenuity can devise of discovering at what depth the coral formation begins, and of what materials the substratum on which it rests is composed. The shape, slope, and elevation of the coral knolls in the lagoon would also help the investigation; and no circumstances should be neglected which can render an account of the general structure clear and perspicuous. (Extract from "memorandum" in Fitzroy, 1839, p. 38).

Charles Darwin's presence on the Beagle's voyage was precipitated by Fitzroy's anxiousness "... that no opportunity of collecting useful information, during the voyage, should be lost..." so Fitzroy "... proposed to the Hydrographer that some well-educated and scientific person should be sought . . . . . Captain Beaufort approved of the suggestion, and wrote to Professor Peacock, of Cambridge, who consulted with a friend, Professor Henslow, and he named Mr. Charles Darwin, grandson

of Dr. Darwin the poet, as a young man of promising ability, extremely fond of geology, and indeed all branches of natural history." (Fitzroy, 1839, pp. 18–19). In Fitzroy's (1839) list of persons aboard the Beagle when it sailed from England, Darwin was listed as "naturalist."

During the voyage of the Beagle, Darwin visited South America in 1834–1835. He was strongly influenced by Lyell's *Principles of Geology* published in 1832 in which Lyell dedicated the final chapter to coral reefs. (see Chapter *Lyell, Charles (1797–1875)*). Influenced by Lyell's work, Darwin noted the effects of intermittent uplift on the land together with erosion and deposition of sediments. From this, he speculated on the effects of subsidence upon the upward growth of corals and made some outstanding deductions before he had ever seen a coral reef. He deduced that progressive island subsidence could transform a fringing reef into a barrier reef and finally into an atoll. According to Harvey (1982, p. 3) Darwin's deductive model was confirmed when he visited Tahiti in November 1835 and viewed the island of Moorea from the neighboring slopes behind Papeete. He saw the central volcanic island surrounded by a lagoon, which in turn was encircled by a barrier reef. He deduced that with progressive subsidence of the central volcanic island the encircling reef would slowly grow upwards until the central lagoon had disappeared altogether leaving only a circular rim of coral with a central lagoon. Thus, the theoretical development of fringing reefs to barrier reefs and finally to atolls overcame the problem of explaining the anomalously great depths at which shallow water reefal limestones had been found.

The same sequence of reef development was not readily applicable to continental margin reefs such as the Great Barrier Reef (GBR). Harvey (1982) notes that Darwin never visited the GBR although following the visit to Tahiti, the Beagle on her homeward journey sailed around the southern shores of Australia. Darwin did, however, attempt to relate his subsidence theory to the GBR, suggesting that it "may have been important in the Reef's evolution. Although he was not able to test this hypothesis, the importance of his subsidence theory deduced from Pacific atolls and the debate that followed its publication had a profound effect upon research in the Great Barrier Reef Province" (Harvey, 1982, p. 3).

## A deductive theory

As noted by Chancellor and van Wyhe (2008) and Harvey (1982), Darwin's ideas on coral reefs had been formed before he had seen one. Chancellor and van Wyhe (2008) comment that Darwin's "Santiago Notebook" "...has been quoted from by many scholars in connection with the famous passage which confirms that Darwin had thought out his coral reef theory before seeing a coral island, as he claimed in his *Autobiography*...". In the autobiography, Darwin wrote:

No other work of mine was begun in so deductive a spirit as this; for the whole theory was thought out on the west coast of



S. America before I had seen a true coral reef. I had therefore only to verify and extend my views by a careful examination of living reefs. But it should be observed that I had during the two previous years been incessantly attending to the effects on the shores of S. America of the intermittent elevation of the land, together with denudation and the deposition of sediment. This necessarily led me to reflect much on the effects of subsidence, and it was easy to replace/in imagination the continued deposition of sediment by the upward growth of coral. To do this was to form my theory of the formation of barrier-reefs and atolls. (Darwin, 1958, pp. 98–99)

## Second edition of “Coral Reefs”

In 1874, a revised second edition of *Coral Reefs* was published. Darwin writes that in the second edition, he has “added some new facts and have revised the whole book; the latter chapters having been almost rewritten” (Darwin, 1874, p. viii). According to Freeman (1977), this was influenced by the work of Professors Dana and Jukes. Certainly, Darwin writes that since the 1842 publication, “only one important work on the same subject has appeared, namely, in 1872, by Professor Dana, on *Corals and Coral-Reefs*”. In the preface, he discusses some of Dana’s assertions and criticisms of his (Darwin’s) work. Of Professor Dana, Darwin comments that

Although I thus demur to some of the remarks and criticisms made by this eminent naturalist, who has examined more coral formations than almost any other man, yet I do not the less admire his work. It has also afforded me the highest satisfaction to find that he accepts the fundamental proposition that lagoon islands or atolls, and barrier-reefs, have been formed during periods of subsidence (Darwin, 1874, p. vii).

Darwin, in the preface to the second edition, quotes Jukes as saying Darwin’s “hypothesis is perfectly satisfactory to my mind.” However, Darwin suggested that the “distinguished naturalist, Professor Semper, differs much from me, although he seems willing to admit that some atolls and barrier-reefs have been formed in the manner in which I suppose” (Darwin, 1874, p. vii).

## Conclusions

Although the basics of Darwin’s theory have since been proven by deep borings and geophysical surveys on many open ocean atolls, his theory initiated a great deal of debate centered mainly around the substrate from which reefs grew. This debate resulted in alternative theories (see Chapter *Subsidence Hypothesis of Reef Development*) or new ideas which added to Darwin’s theory. While there are various reviews of these (e.g., Cotton, 1948; Harvey, 1982; Hopley, 1982) the fundamentals of his theory remain, and Darwin’s works represent perhaps the most important nineteenth century contribution to the study of coral reefs.

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Lyell, Charles (1797–1875)  
 Subsidence Hypothesis of Reef Development

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## DAVID, TANNANT EDGEWORTH (1858–1934)

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Professor of Geology at the University of Sydney (1891–1924), Tannant Edgeworth David was born in St. Fagans, South Wales as the eldest child of the Rev. William David and his wife Margaret Harriette, née Thomson, from whose family came the names Tannant and Edgeworth.

David entered New College, Oxford in 1876 and gained a first class in classics in 1878; however, a breakdown in health prevented him from reading for final honors. While convalescing, he traveled to Canada and then on a round trip to Melbourne in the sailing ship *Yorkshire*. Back at Oxford, David attended Professor Joseph Prestwich’s lectures on geology before graduating



**David, Tannant Edgeworth (1858–1934), Figure 1** David, Tannant Edgeworth.

B.A. in 1881 (M.A. 1926). He returned to Australia in 1882 on the steamship *Potosi* arriving at Sydney on the 27th November to join the New South Wales Government as assistant geological surveyor. He married Caroline Martha (Cara) Mallett on the 30th July 1885 at St Paul's Church of England, Canterbury, having met her earlier on the voyage to Sydney in 1882. Edgeworth David joined the University of Sydney as Professor of Geology and William Hovell Lecturer in Physical Geography in 1891 (Figure 1).

Within his first decade as Professor at the University of Sydney, Edgeworth David enjoyed world wide repute, chiefly as a result of his work on Funafuti Atoll in the Ellis Islands. Always the opportunist, David saw as a challenge the 1896 failure of the party sent by the Royal Society of London to bore a deep section at Funafuti. Excited by Darwin's 1842 assertions that coral reefs were shallow water structures built on sinking foundations, Edgeworth David raised the necessary funds for an expedition from Sydney equipped with diamond drills made available by the New South Wales Government: the scientific objective was to drill a deep hole through the reef to test this assertion. In June 1897, David left for Funafuti, accompanied by his wife Mrs. Cara David, George Sweet (a practical engineer and amateur scientist), two senior students, and a party of workmen. After many difficulties, not all of them mechanical, the drilling reached a depth of 177 m before David returned to Sydney, leaving Sweet in charge; thereafter, Mr. Sweet extended the hole to a depth of 213 m before the workmen refused to continue. The following year, David sent another party to "finish the job" and the party cleaned and deepened the hole to a final depth of 339 m.

The drilling showed conclusively, both at the time and since, that the entire section drilled to 340 m is comprised of shallow water organisms; indeed, the first indications of the importance of *Halimeda* in producing carbonate came from cores taken at Funafuti Atoll in 1904. A core drilled into the reef to a depth of 339 m was mostly composed of *Halimeda* and other calcareous algae. This evidence gave striking support for *Charles Darwin's* theory that coral atolls had grown progressively under the influence of subsiding platforms. It did not however show that the subsiding platforms were volcanic based, a conclusion proved much later in the mid-twentieth century.

Although the main technical reports on Funafuti did not appear until 1904, David's part in the venture was recognized by the award of the Bigsby medal by the Geological Society, London, in 1899; next year the Royal Society, London, admitted him a fellow. Mrs. Cara David published an "unscientific account" of the expedition, *Funafuti: Or, Three Months on a Coral Island* (1899).

Following the Funafuti work, David worked in Antarctica with Shackleton and was the first to the south Magnetic pole; he later mapped the New South Wales coal fields, directed the Allies underground Trench systems in the 1914–1918 War and wrote the definitive first work on the Geology of Australia. He was knighted in 1920 and became known as Sir Edgeworth.

Tannant Edgeworth David retired from the University of Sydney in 1924 and died in Sydney in 1934 at the age of 76.

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## Cross-references

[Atolls](#)  
[Darwin, Charles \(1809–1882\)](#)  
[Funafuti Atoll](#)  
[Reef Drilling](#)  
[Subsidence Hypothesis of Reef Development](#)

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## DAVIS, WILLIAM MORRIS (1850–1934)

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American geographer, geologist, meteorologist but fundamentally the leading figure in the development of the

study of landforms – geomorphology – between the 1880s and 1930s.

### Davis and Coral Reefs

William Morris Davis (1850–1934) was the dominant figure in the development and codification of geomorphology (the science of the study of landforms and the processes that form them) from the last decades of the nineteenth century, responsible for the concept of the “cycle of erosion” whereby landforms pass progressively, irreversibly, and predictably through the stages of “youth”, “maturity”, and “old age”. Following his resignation from the Sturgis Hooper Professor of Geology at Harvard University in 1912 (where he was succeeded by R. A. Daly), his scientific focus became strongly reef-based; he published over 50 items on coral reefs between 1913 and 1934, including a major treatise, ‘The Coral Reef Problem’, published in 1928. Much of this work was desk-based and theoretical, but he undertook a 9 month cruise to Pacific reefs in 1914 (including visits to Hawaii, Fiji, New Caledonia, the New Hebrides, New Caledonia, and the Great Barrier Reef (where a visit to Green Island, Great Barrier Reef was dismissed as “an entertaining experience, but, as might have been expected, entirely fruitless as far as the origin of the reef is concerned” (Davis, 1928, p. 347)), Rarotonga and Tahiti) and a shorter visit to the Caribbean in 1923. He was totally supportive of Darwin’s subsidence theory, promoted J. D. Dana’s “principle” of the importance of the embayed shorelines as evidence for volcanic island subsidence and made useful observations on the cliffs of volcanic islands on the margins of the reef seas, which he attributed to a lack of reefal protection during glacial stages. As P. B. King perceptively pointed out (see King and Schumm, 1980), his analysis had most conviction when dealing with the relatively simple tectonic settings of oceanic reefs but struggled elsewhere. Thus, as Stoddart (1994) has argued, he systematically misrepresented the geomorphic history of elevated reef islands in Fiji, Tonga, the Loyalty Islands and the southern Cook Islands, from no or very limited field observations, erroneous assumptions on erosion rates and the removal of limestone topography, and by ignoring paleontological evidence for the antiquity of exposed raised limestones.

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 Darwin, Charles (1809–1882)  
 Stoddart, David Ross (1937–)  
 Subsidence Hypothesis of Reef Development

## DENSITY AND POROSITY: INFLUENCE ON REEF ACCRETION RATES

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Estimations of coral reef accretion rates can be undertaken using a number of techniques. Most tedious is the use of growth rates from individual organisms (Chave et al., 1972). More recent methods include the measurement of total reef metabolism and calcification (Kinsey, 1985) or estimates of rates during the Holocene from dated drill cores (Davies, 1983; Davies and Hopley, 1983).

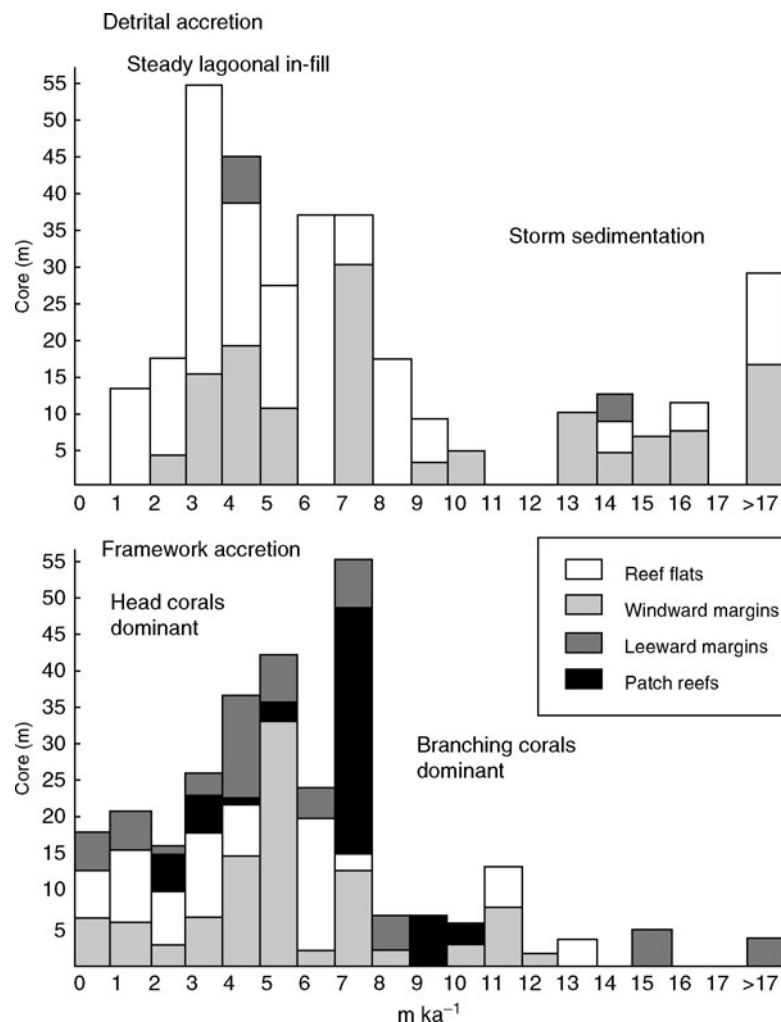
Alkalinity anomaly measurements can be made for different zones of the reef. However, in transforming results, from kg m<sup>2</sup>/year into vertical accretion rates, differences in specific gravity (S.G.) of different elements of the reef need to be considered. Elements such as corals, molluscs, codiaceans and *Halimeda* are composed of aragonite (S.G. 2.94) while coralline algae, foraminifera and bryozoans are mainly magnesium calcite (S.G. 2.72).

Producing even greater variability in the conversion is the porosity of the reefal fabric. Coral colonies have bulk densities of 1.0–2.2 g/cm<sup>3</sup>, (Buddemeir et al., 1974). The reef fabric in drill cores has a wide range of porosities from very low (where internal cavities have been infilled with marine cements) to very high, in branching coral framework. Nonetheless, the results from drill cores are remarkably similar to those obtained from reef metabolism studies, where a porosity value of 50% is normally assumed, (Smith, 1983).

Vertical accretion rates (Figure 1) vary up to 16 m/1,000 years with the mode around 7–8 m/1,000 years obtained from both alkalinity studies and drill cores. Reef fabric porosity plays an important role in both framework and detrital deposition. Higher rates in framework are mainly from open branching corals, lower rates from head corals and algal crusts. Within detrital facies two distinct groupings occur:

- 1–9 m/1,000 years representing steady, mainly fine grained accumulation during normal stormy weather.
- Extremely high rates of 13–18 m/1,000 years from coarser more porous gravel sheets deposited during short periods of cyclonic weather.





**Density and Porosity: Influence on Reef Accretion Rates, Figure 1** Rates of vertical detrital and framework accretion throughout the Holocene based on dated cores (from Davies and Hopley, 1983; Hopley et al, 2007). Porosity of materials laid down strongly influences accretion rates and these in turn have a correlation with energy levels and location on the reef. (Courtesy of Cambridge University Press).

Changes to these figures occur through time. Greater porosity may result from bio-erosion while denser framework results from compaction and deposition of marine cements.

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## Cross-references

[Aragonite](#)

[Calcite](#)

[Carbonate Budgets and Reef Framework Accumulation](#)

[Porosity Variability in Limestone Sequences](#)

## DEVONIAN REEF COMPLEXES OF THE CANNING BASIN

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Middle and Upper Devonian reef complexes are spectacularly exposed along the northern margin of the Canning Basin. They form rugged limestone ranges, in a belt some 350 km long and up to 50 km wide, that have become known as the “Devonian Great Barrier Reef.” (Figure 1).

The barrier-reef system formed as fringing reefs, atolls, and banks, which grew along the mountainous mainland shore of the Kimberley block and around rugged islands of Proterozoic igneous and metamorphic rocks. The maximum thickness of the Devonian rocks is estimated to be at least 2,500 m (Figure 2).

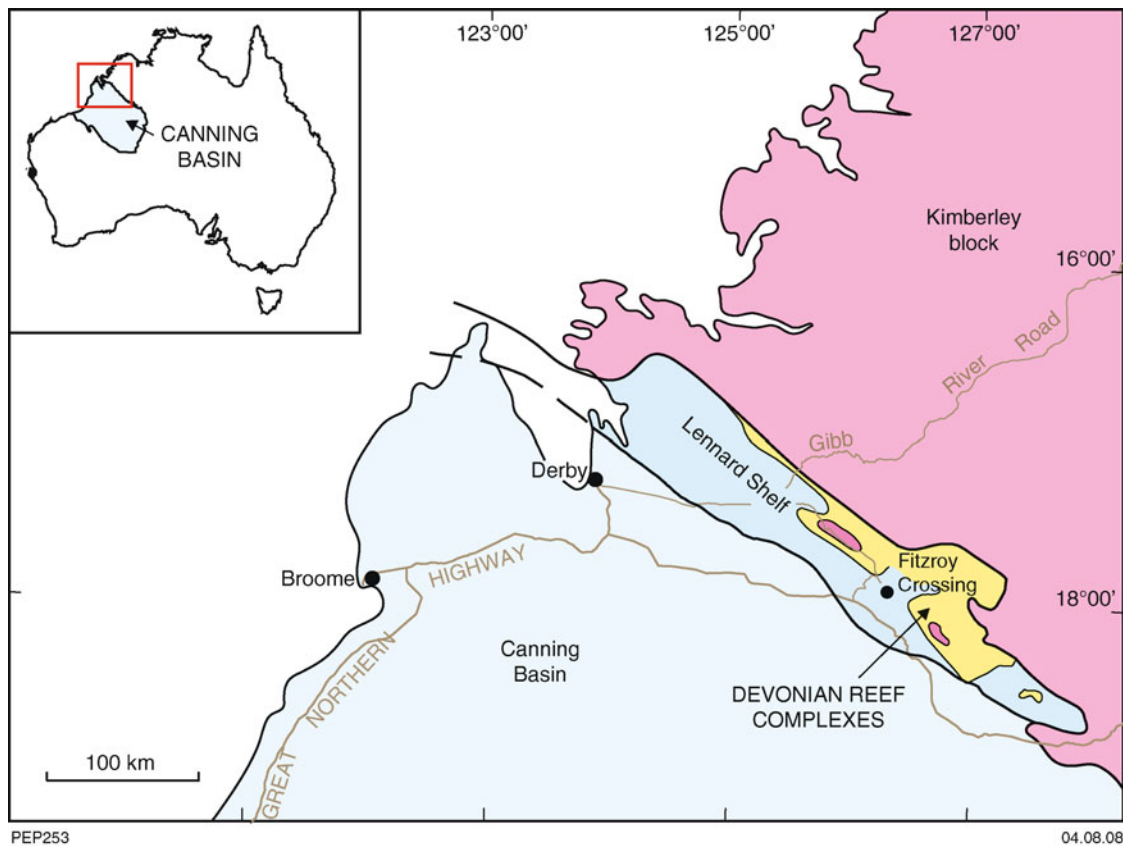
Three main facies are recognized in the reef complexes: platform, marginal slope, and basin facies. Most platforms were rimmed by rigid wave-resistant reefs. The reefal platforms stood tens to hundreds of meters above the adjacent seafloor, and were constructed by shallow-water organisms: mainly stromatoporoids, corals, and microbes

during the Givetian and Frasnian, and microbes during the Famennian (Figure 3).

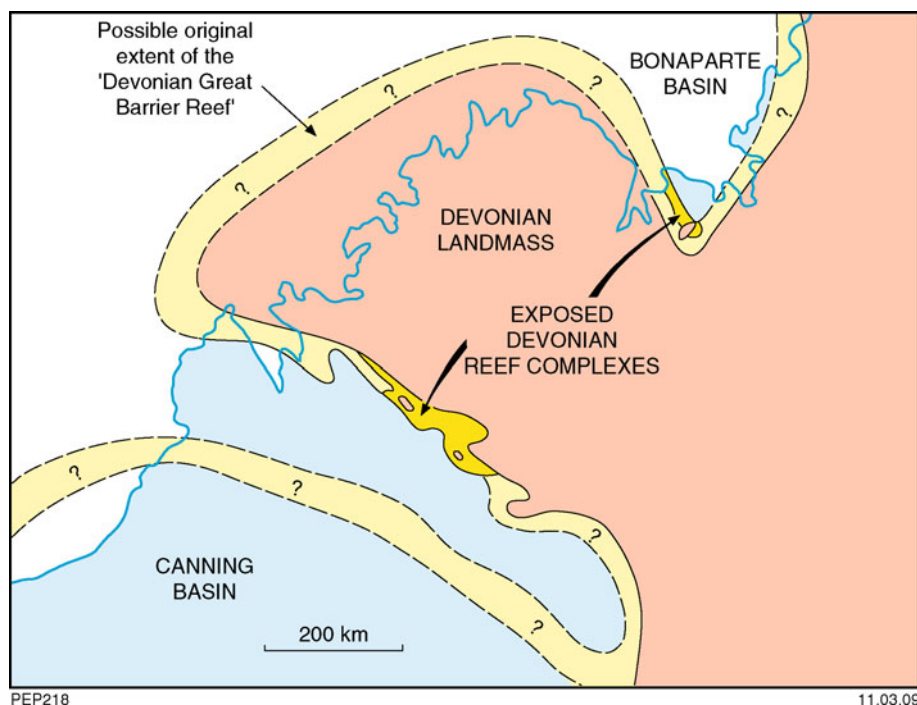
The platform deposits were laid down essentially horizontally, in shallow subtidal to intertidal and supratidal environments, while the marginal-slope deposits, consisting largely of platform-derived debris, were formed on steep slopes in front of the platforms, reaching depths of up to several hundred meters. The basin facies, which was laid down essentially horizontally, consist largely of calcareous shale, siltstone, and sandstone.

The reef complexes range in age from Middle Devonian (late Givetian) to late Devonian (Frasnian and Famennian). The most precise datings are based on conodonts and ammonoids in basin and marginal-slope deposits. The platforms were retreating (retrograding) and backstepping during the Givetian to late Frasnian, and advancing (prograding) during the latest Frasnian and Famennian. This pattern may have been linked to a long-term rise and fall in global sea level. The Frasnian–Famennian boundary marks the culmination of a global mass extinction of meta-zoan organisms (Figure 4).

Third-order sequences, associated with backstepping of the platforms, are thought to be linked with episodes of faulting. The rigid early cemented reef limestones were



**Devonian Reef Complexes of the Canning Basin, Figure 1** Locality map, Devonian reef complexes of the Canning Basin, Western Australia. (From Playford et al. [2009].)



**Devonian Reef Complexes of the Canning Basin, Figure 2** Map of the Kimberley district showing the possible original extent of the "Devonian Great Barrier Reef." (From Playford et al. [2009].)



**Devonian Reef Complexes of the Canning Basin, Figure 3** Aerial view of the northwestern Napier Range reef complex, looking southeast. The reef complex winds across the countryside, mimicking its form during the late Famennian. Conglomerate of the Van Emmerick Conglomerate underlies and interfingers with the reef complex, forming the rounded hills in the left middle distance. (From Playford et al. [2009].)

subjected to fissuring in response to contemporary earthquake shaking, slippage along underlying marginal-slope deposits, and differential compaction over buried basement topography. The fissures were filled with sediment,

calcite cement, and organic growths, forming networks of neptunian dykes.

The lithologies of the reef complexes have remained essentially unaltered since deposition, other than in about





**Devonian Reef Complexes of the Canning Basin, Figure 4** Aerial view of the Napier Range at Windjana Gorge looking northwest. The sinuous front of the range is essentially the late Famennian reef scarp. (From Playford et al. [2009].)



**Devonian Reef Complexes of the Canning Basin, Figure 5** Aerial view looking north over the Laidlaw Range reef complex, showing its "tail" of Glenister Knolls patch reefs (arrow 1). On the left are Smith Knoll pinnacle reef (arrow 2), Lloyd Hill atoll (arrow 3), and Wade Knoll pinnacle reef (arrow 4). Ross Hill (arrow 5) is composed of Lower Permian sandstone, which unconformably overlies the reef complex. (From Playford et al. [2009].)

15% of the section where early dolomitization occurred. In some areas, the reef complexes are cut by normal faults, with associated tilting and folding, but over large areas, they remain almost undeformed (Figures 5 and 6).

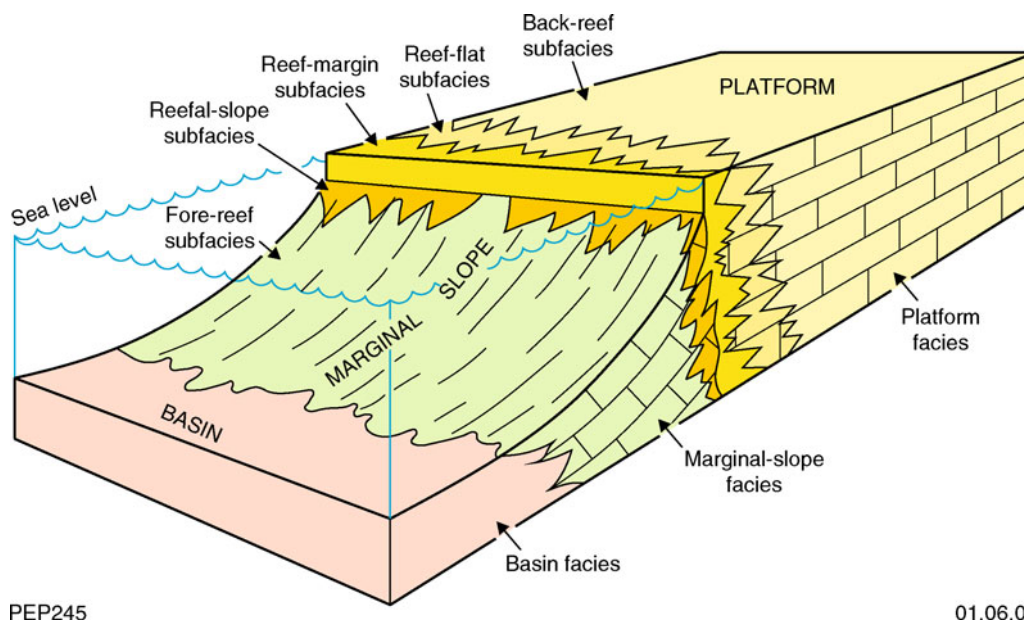
Masses of terrigenous conglomerate interfinger with and extend through the reef complexes at various localities along the outcrop belt. They were laid down as

alluvial-fan, fan-delta, and submarine-fan deposits in front of the scarps of active faults. Large volumes of sand and mud were poured into basins adjoining the conglomerate bodies (Figure 7).

The area was subjected to glaciation during the late Carboniferous and early Permian, by continental ice sheets, possibly up to several kilometers thick. Glaciation



**Devonian Reef Complexes of the Canning Basin, Figure 6** Aerial view, looking south, toward the Classic Face at Windjana Gorge, showing wepp-bedded, low-dipping, platform limestones of the Pillara Limestone on the right, massive reef-margin and reefal-slope limestones in the center, and steeply dipping fore-reef limestones of the Napier Formation on the left. (From Playford et al. [2009].)



**Devonian Reef Complexes of the Canning Basin, Figure 7** Block diagram illustrating the morphology of the reef complexes and relationships between platform, marginal slope, and basin facies and the various subfacies. (From Playford et al. [2009].)

had profound effects on the Devonian rocks. The tops of the limestone ranges were planed off by “dirty” ice at the base of the ice sheets and were extensively karstified by the corrosive action of subglacial water under high pressures and subzero temperatures.

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## DIAGENESIS

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### Definition

The biological, physical, and chemical processes occurring concomitantly or separately in time and modifying a sediment during and after its deposit.

### Introduction

Reefs have caused a tremendous interest in diagenetic studies in the past decades, with a particular exponential development during the 1970s and 1980s, just after the major discovery of the early submarine cements in modern coral reef complexes in the late 1960s (Ginsburg et al., 1967; Macintyre et al., 1968; Land and Goreau, 1970).

In the general topic of carbonate diagenesis, reefs represent highly favorable systems for the study of diagenetic processes because they are especially susceptible to diagenesis occurring either in marine, mixed, or nonmarine waters, and as sedimentary systems, they have relatively clearly defined geometries. Another reason explaining their scientific interest is their reservoir potential, and from this point of view also, the precise analysis of reef-limestones diagenesis is of critical importance for the assessment of their economic significance.

Independently from their age and setting, reefs present several fundamental specificities as regards carbonate diagenesis:

1. They are formed with a very high primary porosity.
2. They are lithified at their time of growth, this limiting the effects of compaction and hence permitting the preservation of initial porosity.
3. Reef facies are usually composed of chemical unstable minerals, such as aragonite and high-magnesian calcite (HMC), which can easily undergo various chemical and mineralogical changes through interaction with circulating pore fluids.

The aim of this encyclopedia is to focus on modern reefs. For this reason, the diagenetic features and processes described here are related to the early diagenesis in the sense of syndepositional diagenetic processes and do not include those depending on burial diagenesis.

### General approach and technical methods

Research in carbonate diagenesis has used, and is still using, a process-based approach, i.e., relying on the identification of processes producing the diagenetic modification, in contrast to the general analogy-based approach classically used in geology and more particularly in stratigraphy and facies studies.

While laboratory experimentation on precipitation–dissolution of the different carbonate species under strictly controlled physicochemical conditions has potentially proved to be of great help for our understanding of the mechanisms involved in carbonate diagenesis, a purely physicochemical approach alone cannot provide the keys for deciphering the highly diverse diagenetic pathways and their effects on the studied carbonate system through time and space. This is mainly due to the fact that the interior of a reef is a strongly dynamic system involving many interactions of biological, physical, and chemical processes and important movements of water masses facilitated by the high porosity and permeability typical of reef facies.

The usual approach is preliminarily based on a petrographical analysis of thin sections under the optical microscope, combined with SEM observations and geochemical characterization of the identified diagenetic products. Complementary observations and analyses involving various sets of more sophisticated techniques may be further undertaken depending on the scientific questions arising from the first results and on the specific objectives of the study concerned. The improvement and development of analytical techniques in recent years provide us with a large spectrum of potential analyses encompassing the fields from biochemistry to mineralogy.

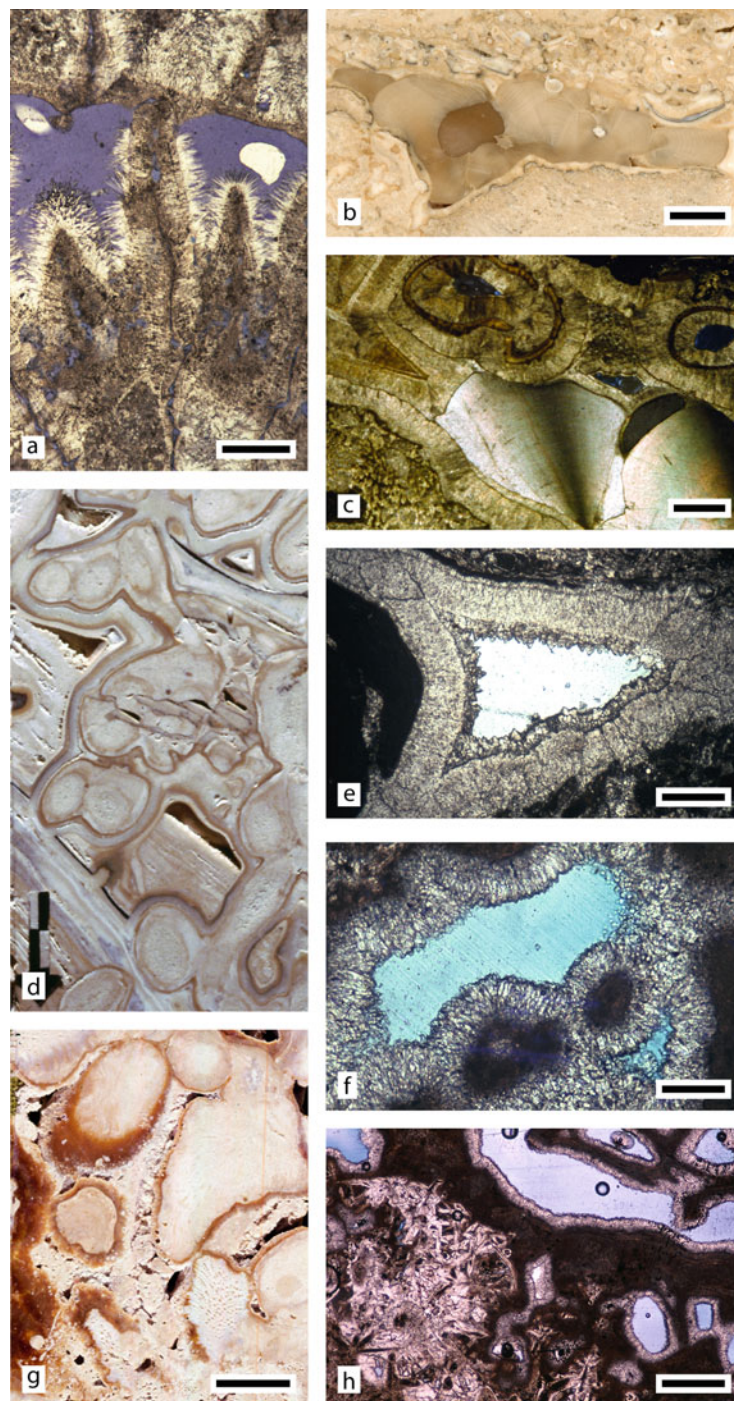
### Cementation

#### Early cements

##### *Early cements in recent reefs*

*Aragonite cements* are frequently developed in Holocene, including present day and Pleistocene coral reefs. Two distinct types of aragonite cements are commonly recognized: the needlelike or acicular aragonite cement (Figure 1a) and the botryoidal aragonite (Figure 1b and c). The first type of cement has been frequently described in numerous studies of recent reefs and numerous terms have been used to describe the various morphologies of this cement (Ginsburg et al., 1971; Ginsburg and Schroeder, 1973; Schroeder, 1972; Bricker, 1973; James et al., 1976; Macintyre, 1977; Harris et al., 1985; James and Ginsburg, 1979). The acicular crystals are typically 2–10 µm wide and 50–300 µm long with pointed terminations, elongated parallel to the crystal's *c*-axis and having straight extinction (Aïssaoui, 1986). The morphological varieties of this cement include acicular crystals occurring as isopachous fringes, bladed crystals, fanlike needles, and needle meshworks, like those described in Belize (James and Ginsburg, 1979). The acicular cement frequently forms a relatively loose structure resulting from the sometimes irregular disposition of crystals. It can also consist of epitaxial overgrowths of aragonite substrates, usually aragonitic mollusks or coral fragments (Figure 1a). The distribution of this cement has often been shown to be very heterogeneous, even within the same thin section, with some primary voids completely filled up with this cement and the neighboring pores entirely devoid of aragonite needles.





**Diagenesis, Figure 1** Early marine and nonmarine cements, Mururoa Atoll, Holocene and Pleistocene reef facies. (a) Aragonite acicular cement forming epitaxial overgrowths on aragonite scleractinian coral skeleton, thin section, scale bar: 250  $\mu\text{m}$ . (b) Botryoidal aragonite cement overgrowing a isopachous high-magnesian calcite (HMC) fibrous cement, polished slab, scale bar: 1 cm. (c) Two botryoids of aragonite cement, thin section, crossed nichols, scale bar: 250  $\mu\text{m}$ . (d) HMC isopachous cement around fragments of coral branches, this cement is overlain by geopetal infills of marine internal sediment, polished slab, scale bar: 2 cm. (e) HMC isopachous fibrous cement followed by a thinner layer of sparitic low-magnesian calcite (LMC) cement, thin section, scale bar: 300  $\mu\text{m}$ . (f) HMC isopachous bladed palissadic cement, thin section, scale bar: 300  $\mu\text{m}$ . (g) LMC karstic brown calcite cement, the cement is affected by boring marine organisms (lower left corner of photograph) and overlain by marine bioclastic sediment, polished slab, scale bar: 2 cm. (h) Needlelike or whisker LMC calcite cement typical of calcrete pedogenetic facies, here associated to a characteristic alveolar texture, thin section, scale bar: 500  $\mu\text{m}$ .

The botryoidal aragonite cement (Figure 1b and c) was first described from Holocene sediments of the Persian Gulf (Shinn, 1969), from Bermuda cup reefs (Schroeder, 1972) and from the Holocene reef of Belize (Ginsburg and James, 1976). Pleistocene examples have also been described in details from the Red Sea, Loyalty Islands (Ouvea), and Mururoa Atoll by Aïssaoui (1985), Aïssaoui and Purser (1985), and Aïssaoui et al. (1986). The botryoidal aragonite cement forms individual and/or coalescent knolls of compact fibrous aragonite crystals with a spherulithic arrangement (Figure 1b and c). These botryoids vary in size between one to several centimeters until tens of centimeters in diameter and they have a typical translucent honey brown color in section. Petrographically, it appears that each fan of aragonite fibers presents a typical sweeping extinction under crossed nichols (Figure 1c). The individual crystals forming these fans are euhedral fibers 2–10  $\mu\text{m}$  in diameter and several hundreds of microns in length. The botryoidal aragonite cement occurs in reef open cavities, usually on the reef wall or reef slope, where it can alternate with internal marine sediment or even be affected itself by marine microborings. From the various examples described in the literature, there is no evidence of substrate control, as the aragonite botryoids were observed growing on calcite, including HMC (Figure 1b), or aragonite substrates. The Sr content of this aragonite cement is about 8,000–10,450 ppm and hence characteristic of an aragonite precipitated from normal marine waters. The composition in other trace elements and stable carbon and oxygen isotopes analyzed from the Holocene and Pleistocene botryoidal cements is also in good agreement with a precipitation from normal marine water (Ginsburg and James, 1976; Aïssaoui, 1986), although Aïssaoui (1986) described a Miocene aragonite botryoidal cement of karstic origin.

*High-magnesian calcite (HMC) cements* commonly constitute the most frequent and most volumetrically important cements in Holocene and Pleistocene reef frameworks (Figure 1d), and have been largely described in the literature. HMC cements are morphologically much more diverse than their aragonite counterparts, with morphologies ranging from fibrous and palissadic types to sparitic and micritic cements.

The fibrous HMC cements (Figure 1e) form single or several isopachous successive layers fringing primary inter- or intra-granular voids. The thickness formed by several cement layers can reach a few centimeters in some cases, such as in the Mururoa Atoll rim (Repellin, 1977; Buigues, 1982; Aïssaoui, 1986). In thin sections, they show a compact bundle arrangement, each individual bundle presenting a sweeping extinction under crossed nichols. Individual crystallites forming the bundles are not clearly distinguishable, even under the SEM. They correspond to fibers of several tens to hundreds of micrometers length, having anhedral shapes and grouped together in divergent units, several of them forming the bundle.

Bladelike forms of HMC cements or bladed spar have also been described, particularly in Belize, Mururoa, and Loyalty Islands (James and Ginsburg, 1979; Aïssaoui, 1986; Carrière, 1987). They consist of elongated crystals with angular terminations and triangular sections, which currently form palissadic layers (Figure 1f). Individual calcite crystals are typically of 20–50  $\mu\text{m}$  width for a few hundreds of microns in length. The bladed HMC type commonly occurs together with the fibrous HMC cement in the same facies and even in the same void, in addition, lateral gradation from one form to the other has already been described.

HMC sparite or stubby spar cements seem to be less common and mainly restricted to small intergranular voids in Belize and Mururoa. This cement forms isopachous fringes composed of broadly triangular crystals, a few tens to hundreds of microns large, gradually widening from the substrate upon which they grow toward the pore center. Under SEM, each calcite crystal appears composed of many thin elongated crystallites, with hardly discernible external limits. This type of cement can be considered as a variety of the bladed-spar cement.

A different blocky HMC sparite forming mosaics of equant 20–60  $\mu\text{m}$  crystals has been also described in Bermuda and Bahamas reefs (Schroeder, 1972; Pierson and Shinn, 1985) and has been also considered as precipitated from open marine waters. This cement seems, however, to be relatively rare.

HMC micrite cements are ubiquitous in most Holocene and Pleistocene reefs although its volumetric importance is highly variable from one site to the other. The magnesian micrite cement consists of small curved-face rhombs, a few microns in size, forming a thin layer about 10  $\mu\text{m}$  thick, lining surface grains. They should be distinguished from micritic envelopes resulting from the algal-microbial micritized external parts of bioclasts. As underlined by James and Ginsburg (1979), this cement seems to be, in most cases, the first to precipitate and may be followed by any other type of early cement, either calcite or aragonite. It should be noted, however, that when this cement is abundant, the questionable origin of micrite as cement precipitated from seawater or deposited lime mud, starts to be a true problem.

Their Mg content of these cements usually varies between about 10 to more than 15 mol%  $\text{MgCO}_3$ , in most of the Quaternary reefs described in the literature. In the Mururoa reef facies, there is a good correlation between the mean Mg content and the type of cement, with cements formed of fibrous or elongated crystals bearing the highest Mg content, which confirmed the effect of Mg on the development of fibrous calcite shown by the experiments of Badiozamani et al. (1977) on carbonate precipitation (Aïssaoui, 1986). The geochemical composition of HMC cements, including trace elements and stable isotopes of carbon and oxygen, is largely considered as in accordance with a marine origin.

*Low-magnesian calcite (LMC) cements* are common although usually not forming an important volume of the

limestone mass in Quaternary reefs. They are restricted to particular horizons in the reef rock and usually considered as resulting from a diagenesis related to subaerial environment. They are, therefore, linked to some degree to subaerial exposure of the reef body during emersions and, hence, can be precipitated either directly on emerged surface substrates or at depth within the reef rock in relationship with circulation of interstitial fluids. In both case, they have a nonmarine origin as shown by their low-magnesium content and their isotopic signature. The most frequent morphological types include needlelike calcite cement and a great diversity of sparite cements.

The needlelike or whisker calcite cement (Figure 1h) is developed in calcrete (caliche) pedogenetic facies and is often associated with the characteristic alveolar texture formed by networks of interconnecting micrite walls representing rhizoconcretions or rhizoliths. This calcite is composed of single fibrous crystals often forming a loose meshwork and displays a variety of habits and arrangements of individual crystals. The precise origin of this typical cement has been questioned for past decades to know if it results from direct precipitation in close relation with the high degrees of supersaturation caused by physicochemical changes in soil profile or if it has a biogenic, possibly microbial origin, and this is still a matter of debate (Goudie, 1996; Cailleau et al., 2009).

The mosaic sparite cement consists of large size (from 100  $\mu\text{m}$  to more than 1 mm) limpid crystals either with a thick and irregular shape or slightly more elongated with euhedral terminations. It fills up partially or completely primary or secondary intra- and inter-granular voids.

The elongated-crystal sparite or brown calcite cement (Figure 1g) is formed by individual elongated crystals widening toward the center of the cavity within which they develop, and having pyramidal terminations. The sometimes important development of these cements in relationship with emersion surface and karstic processes clearly demonstrate their subaerial origin, also corroborated by their trace element and isotopic composition.

#### *Early cements in ancient reefs*

Ancient reefs commonly have undergone successive steps of various diagenetic processes, including diverse phases of cementation, linked to the changing physicochemical conditions and supersaturation state in pore fluids during their geological history. As a result, in this chronology, each diagenetic phase provides new diagenetic products and affects in some degree the preexisting materials of sedimentary, biological, and diagenetic origins. While the relative chronology of cements in ancient reefs can be established from detailed petrographical analyses, their original mineralogy and geochemical composition have to be deduced through interpretation of available data.

*Botryoidal cements* in ancient reefs and carbonate platforms are relatively common and have been described from Precambrian to Cenozoic formations. While their

morphology and size are similar to their counterparts occurring in recent reefs, they differ significantly in terms of their current mineralogy and petrography. Ancient botryoidal cements are formed by LMC sparite resulting from the calcitization of the original fibrous aragonite, as shown by the frequent presence of aragonite relics included in the spar crystals (Mazzulo and Cys, 1979; Mazzulo, 1980; Aïssaoui, 1985). Diverse origins have been demonstrated for these ancient botryoidal aragonite cements.

*Fibrous cements* represent frequent syndimentary cements in ancient reefs and non-reef carbonate platforms. They usually form isopachous layers of fibrous crystals, parallel or in fanlike arrangement, in primary voids and often present a sweeping extinction when seen in thin section under crossed nichols. They are usually rich in dark micro-inclusions and depending on their diagenetic alteration, a sparitic structure can be overprinted upon the original fibrous arrangement. Most ancient fibrous cements have not preserved their original mineralogy and are formed by LMC. In the lower part of the carbonate formation in Mururoa Atoll, Berbey (1989) has shown that the early marine fibrous HMC cements have undergone a diagenesis leading to the gradual loss of their Mg content, probably by progressive Ca–Mg substitution in the calcite lattice.

*Sparite cements* are generally the most abundant cements in ancient reef facies and usually consist of LMC. Several types can be differentiated from the arrangement and morphologies of crystals and usually the relative chronology of cements can be established for petrographical analysis. However, origins of these LMC sparite cements can be highly diverse, including early diagenesis from surface waters to late burial diagenetic cementation. As there is no *a priori* reliable criterion either geochemical or petrographical, which allows surface/near-surface sparite from deep burial sparite to be distinguished, the precise origin of these cements together with the quality of their parent waters remain extremely difficult to infer, depending mainly on the degree of knowledge of the geological context.

#### **Cementation in reefs**

##### *Role of cementation*

Numerous studies have shown that rapid lithification through syndimentary marine cementation is a widespread feature common to many, if not all, modern tropical corals reefs (Macintyre, 1977; Friedman, 1998) and the development of early cements in ancient reefs is also well known. Therefore, one of the main characteristics of both recent and ancient reefs is that they are being cemented at the time of their growth.

Although the first primary actors in the reef development are undoubtedly the reef-building organisms edifying a rigid mineralized biological framework, early lithification of sediment and cementation of the framework can exert also an important role in the edification of reefs (Purser and Schroeder, 1986). This occurs at



several temporal scales (1) through the contribution of early cements to the rigidity of reef buildups and, hence, the maintenance of the positive relief above the surrounding seafloor sediments and (2) through the high preservation potential of the reef structure in the fossil record.

#### *Distribution of cements*

*At the scale of microfacies*, the variability of cements distribution both in modern and ancient reefs is well known. The distributional pattern of cements at that scale is directly dependent on (1) the amount of water present in the reef porosity and (2) the petrophysical properties (i.e., porosity and permeability) of the reef limestone, while the mineralogical and geochemical characteristics of cements are mainly controlled by the water chemistry. The control exerted by the amount of water is well explained and depends on the position of the considered site relatively to the water table, i.e., phreatic or vadose zones. This affects the amount and distribution of cement being produced: less cement restricted at the lower grain surface or at the contact between neighboring grains in the vadose zone, more cement forming isopachous fringes surrounding grains and lining primary voids in the phreatic zone. The differences in the morphology and distribution of cements occurring at fine scale, even between adjacent pores or within the same thin section, are explained by fine-scale changes in porosity and permeability, resulting notably from size and interconnectivity between voids. They are consequently extremely difficult to predict or to generalize for modeling. The concept of microenvironment, as used in diagenetic studies of reefs, has been created in an attempt to overcome this problem. The diagenetic microenvironment, defined as the fine-scale environment within which diagenetic processes are taking place, is characterized both by its chemical and petrophysical properties.

**At the scale of the reef complex.** The intense marine cementation along the seaward margins of reef complexes has been largely evidenced in a multitude of modern examples throughout the world and belonging to various types of reef settings located both in the Atlantic – Bermuda (Ginsburg et al., 1971), Belize (James and Ginsburg, 1979), South Florida (Lighty, 1985), Jamaica (Land and Moore, 1980), and Galeta Point in Panama (Macintyre, 1977) – and in the Indo-Pacific – the Great Barrier Reef (Marshall, 1986), and Mururoa Atoll and Loyalty Islands (Aïssaoui, 1986; Aïssaoui and Purser, 1985, 1986; Carrière, 1987). The distribution of syndimentary marine cementation is strongly heterogeneous at the scale of the reef complex, with intensely cemented facies on the seaward edges while the leeward and lagoonal sediments remain few or almost not cemented. This has been well illustrated both in uplifted and non-uplifted reef platforms (Aïssaoui, 1986; Carrière, 1987; Figure 2) and conceptualized through the “principle of maximal cementation” (Aïssaoui and Purser, 1985).

Nonmarine cements, related to the history of the reef platform in response to the sea-level changes and periods of emersions, show a very contrasting distribution, concentrated at particular levels following the stratigraphy and from which the importance of cementation is gradually decreasing downward in the reef limestones. This distributional pattern expresses the control of gravity on the circulation of interstitial waters from which the cements are precipitated during the low stands of sea levels (Figure 2).

#### *Controls of cementation*

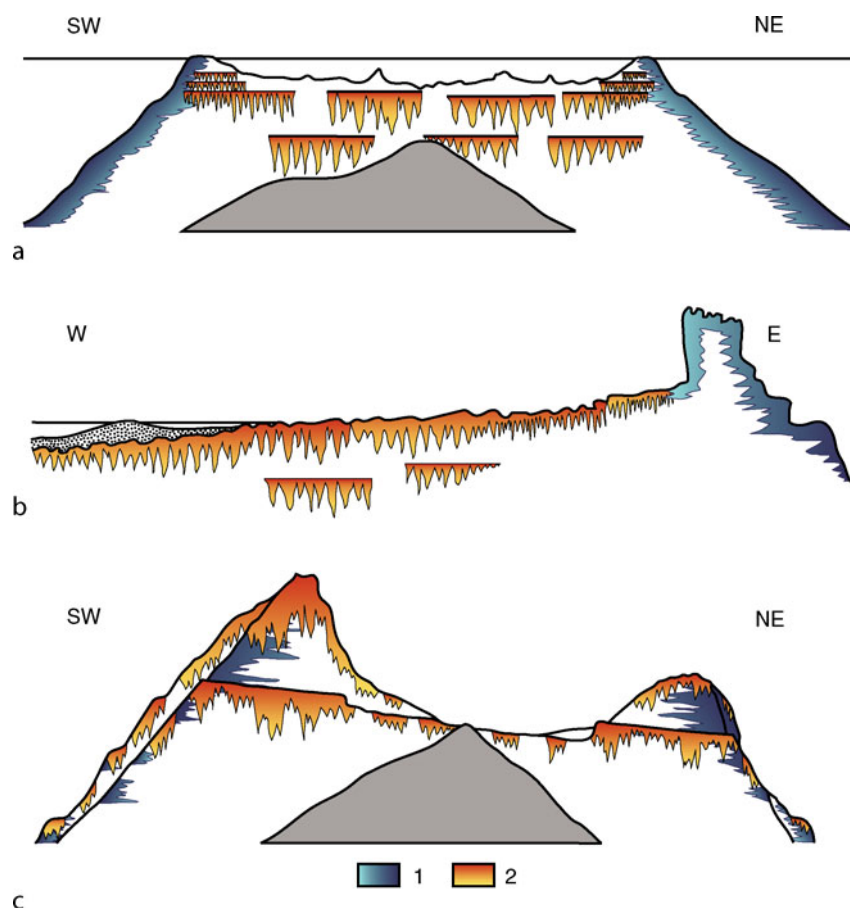
**Control by substrate properties.** The properties of substrate being cemented exert undoubtedly a strong control over the characteristics of the cement itself in some cases, while there is not apparent control in others. The epitaxial overgrowths and syntaxial cement of acicular aragonite are well known to develop preferentially on substrates composed of fibrous aragonite, mainly corals and gastropods in the reef environment. In this case, both the mineralogy and ultrastructure of the substrate control the mineralogy and morphology of the cement. Less frequent examples have also been described for fibrous HMC cement developing upon fibrous calcitic biogenic substrates such as hyaline foraminifera (*Amphistegina*). In thin section, there is usually an optical continuity between the crystals of the substrate and those of the cement.

At slightly larger scale, the petrophysical properties of the substrate seem to control the morphology of HMC cements. Aïssaoui (1986) has shown that there is a good correlation between the elongated shape of cement crystals, itself influenced by the Mg/Ca ratio, and the size of the primary voids being cemented.

**Hydrodynamics.** The asymmetrical distribution of cements is explained by several factors favoring the rapid development of cements along the seaward reef margin, in particular, the higher-energy conditions and cooler oceanic water temperatures, together with the higher permeability and connected porosity of the reef-front facies compared to the fine-grained sediments of the more sheltered back reef or leeward side. The higher-energy conditions on the seaward side are driven by the effect of waves and tides. The higher hydrodynamics on that side allows a large volume of water to pass through the reef framework and an efficient CO<sub>2</sub> degassing to be produced by the warming and moving of the cool open marine waters, resulting in the rapid and significant growth of cements.

#### **Internal sediments**

The link between internal sediment and diagenesis is chronological as the internal sediment is defined as being deposited within the voids of an already lithified substrate. The internal sediment therefore occurs after the first cementation. A certain degree of hydrodynamics is



**Diagenesis, Figure 2** Schematic distribution of early marine cements (1), and nonmarine meteoric cements (2) at the scale of platform or reef complex; volcanic basement in gray. (a) Mururoa Atoll, French Polynesia; (b) The tilted half-atoll of Ouvéa, Loyalty Islands, New Caledonia; (c) The tilted platform/atoll of Maré, Loyalty Islands, New Caledonia. (Modified from Aïssaoui [1986] and Carrière [1987].)

necessary for permitting the sedimentary particles to be introduced and moved within the rock frame. From this point of view, the reefs with their good porosity and permeability, their high susceptibility of early cementation, and their high-energy environmental conditions, are excellent candidates for internal sedimentation.

#### Marine internal sediments

These represent the most frequent internal sediments in modern and ancient reefs. They are generally characterized by their fine-grained bioclastic components and their geopetal arrangement (Figure 1d).

#### Nonmarine internal sediments

These internal sediments are the products of subaerial diagenesis, either in the vadose zone or related to karstic processes during periods of sea-level low stands. Consequently, they represent important discriminant criteria in the reconstitution of reef history and its response to sea-level changes.

#### Vadose internal sediments

*Vadose silts* consist of geopetal accumulations of tiny crystalline debris, produced by the abrasion and mechanical erosion of previously lithified substrates in the meteoric vadose zone. They are frequently associated with sparitic cements and intense dissolution features related to meteoric diagenesis.

*Centrifugal micrite* is not a commonly observed feature in Holocene and Pleistocene coral reefs (Carrière, 1987; Perrin, 1989), certainly due to its narrow zone of occurrence restricted to the supratidal zone (Purser, 1973; Aïssaoui and Purser, 1983).

#### Karstic internal sediments

These internal sediments are filling either primary voids or dissolution cavities sometimes of large size. Their nonmarine origin is attested by the general lack of marine bioclasts, the presence of clays and laminated crusts of pedogenetic origin, together with their typical orange-red color. They may include rock fragments and breccia infilling the largest cavities.

## Dissolution

### Selective dissolution of skeletal elements

The susceptibility of skeletal grains to dissolution is directly related to their mineralogy, their ultrastructure, and their morphology. The bioclasts composed by the most unstable mineralogical phases, such as HMC and aragonite, are obviously the first to be dissolved. However, in details or during the early stages of dissolution, differences are shown between elements of similar mineralogy. This differential susceptibility to dissolution depends on the content in trace elements, notably the ratio Mg/Ca of high-magnesian calcitic bioclasts and on the fine-scale skeletal ultrastructure. This has been well documented for coral skeletons, ultrastructural patterns of which being taxon dependent. Hence, some coral taxa have revealed more sensitive to dissolution than others, and dissolution has been shown to occur preferentially at particular sites, such as trabecular axes and/or median septal plans (James, 1974; Gvirtzman and Friedman, 1977; Constantz, 1986; Dullo, 1986; Perrin, 2004). Additionally, the earliest steps of dissolution evidenced from still living colonies have been demonstrated to occur in the calcification centers, which are more abundant at these particular sites, just a few years after the skeleton being secreted (Perrin and Cuif, 2001). This appears to be strongly linked with the rapid decay of intraskeletal organic matrices more abundant in the centers of calcification (Perrin and Smith, 2007a, b).

### Dissolution of early cements

During the diagenetic evolution of reefs, early cements may be affected by following diagenetic processes including dissolution. Therefore, selective dissolution is not restricted to the biogenic components. Similarly, the mineralogy, morphology, and trace element composition of the cement are important factors controlling its susceptibility to dissolution. Aragonite, HMC, and, even, calcian dolomite cements are variably susceptible to dissolution (Purser and Schroeder, 1986). In the recent reefs of Mururoa and Ouvéa, dissolution of botryoidal aragonite occurs at microstructural scale forming micro-rhomboidal voids visible under SEM (Aïssaoui, 1985, 1986). Various degrees of partial dissolution have been described in the Pleistocene facies of Mururoa Atoll, affecting the isopachous fringes of fibrous high-magnesian calcitic cements (Aïssaoui et al., 1986; Aïssaoui, 1988). However, the irregular dissolution pattern observed or its preferential location at some levels within the thickness of cement layer remain difficult to explain and may be related to a differential original composition of crystals forming the cement (Aïssaoui, 1986).

### Dissolution of dolomite

The dissolution of dolomite or dedolomitization leads to the formation of typical secondary voids which may be common in Holocene, Pleistocene, or older reef rocks. These traces of dedolomitization require to be identified

from thin sections. They are characterized by geometrical voids, a few tens of microns to several millimeters in size, which do not evoke the typical shape of any known bioclast, the smaller voids having often a rhomboedral periphery as does the dolomite crystal. Relics of small crystals of calcian dolomite have been already described on the walls of such secondary voids, hence leaving no doubt regarding their origin (Aïssaoui, 1986). The secondary voids produced by the dissolution of dolomite in reef carbonates can represent a quite important proportion of the total rock, reaching in some cases 40%.

As a consequence, the significance of these dissolution voids is extremely important for the interpretation and reconstruction of reef history and the understanding of reef diagenesis, since this secondary porosity is the only evidence for an earlier stage of dolomitization. As a consequence, dolomitization events have to be characterized through petrographical observations of thin sections and not solely through mineralogical analyses such as x-ray diffractometry, for example. Moreover, the identification of dedolomitization voids may help in the precise reconstruction of the initial geometry of dolomitic bodies (Purser and Aïssaoui, 1985; Aïssaoui, 1986).

### Distribution of dissolution features in reefs

Dissolution in reefs is a ubiquitous process, which often is only detectable at the microscopic or even at the ultramicroscopic scale. The process itself starts at a very early stage, in some cases just after the formation of the carbonate features which is affected by dissolution (Perrin and Cuif, 2001; Perrin, 2004).

Larger-scale dissolution features in reefs are known to occur during sea-level low stands through the exposure of the marine carbonates to the effects of meteoric waters, this leading to the formation of karstic framework and cavities especially under prevalent humid tropical climatic conditions. These macro- to mesoscale dissolution features are distributed at specific horizontal intervals in the ancient reef carbonates and are characterized by open voids, chalky facies, and associated with other meteoric and karstic features (e.g., typical cements and infills).

### Controls of dissolution

The dissolution process is by definition selective in carbonates and this selection is operated through two main controls: the fine-scale ultrastructure and the mineralogy including the trace element composition. The ultrastructure determines the size and arrangement of individual crystals and hence, within a given structure, either biogenic or nonbiogenic, the distribution of crystal boundaries, discontinuities, and crystalline faces which are preferential sites, highly favorable to the initiation of dissolution process. This has been largely evidenced in various groups of skeletal carbonates (Walter, 1985; Dullo, 1986; Flessa and Brown, 1993; Perrin, 2004). In the case of biogenic elements, the intraskeletal organic material (proteins) and its degradation during the early stages of



diagenesis probably play a crucial role in the stability of skeletal carbonates (Perrin and Smith, 2007a, b). This is expressed by the fact that elements of same mineralogy often show various degrees of dissolution depending on the nature and origin of the structure considered: e.g., in some cases aragonite cement may be more resistant to dissolution than their aragonite skeletal substrate (e.g., Scherer, 1986).

### Dolomite in reefs

Reefs are highly susceptible to dolomitization compared to other carbonate facies, as shown by the numerous ancient, including Quaternary, reef bodies and reef platforms which are completely or partially affected by dolomitization. As already emphasized by Purser and Schroeder (1986), the high susceptibility of reefs to dolomitization is the result of a combination of favorable factors such as (1) the important primary porosity and permeability of reef facies, (2) their early history frequently dominated by sea-level changes and therefore rapid evolution of the chemistry of interstitial waters, (3) a high content in metastable minerals, and (4) the presence of organic material.

### Petrography of dolostones

Dolomite may result from different diagenetic processes comprising cementation, replacement of sedimentary or diagenetic precursors, and recrystallization of dolomitic precursors, the three processes occurring often concomitantly in reef facies (Buigues, 1982; Purser and Aïssaoui, 1985; Carrière, 1987; Berbey, 1989). The identification of these processes from petrographical analysis of thin sections permit various dolomite petrotypes to be defined and characterized from geochemical analysis, their distribution within the reef platform to be mapped, and beyond, the interpretation of diagenetic fluids, and the development of dolomitic bodies to be reconstructed.

#### Cementation

In thin section, these dolomite cements are dolosparites characterized by limpid crystals of relatively large size (a few tens to more than 100  $\mu\text{m}$ ), developed in primary and secondary voids, which they may fill completely (mosaic of cement) or partially (fringe of cement).

A quite frequent particular case corresponds to dolomite rhomboedral crystals, typically a few tens of microns, consisting usually of a central darker microcrystalline part resulting from the replacement of a non-dolomitic precursor, and a limpid border, interpreted as the further growth of the same crystalline unit within a void (cementation).

#### Replacement

The replacement dolomites include most of the microcrystalline dolomites, which preserve the detailed shape of bioclasts or previous cements, and most of their texture and consist of small rhomboedral crystals a few microns to 10  $\mu\text{m}$  in size. These replacement dolomites often show a relatively high intercrystalline porosity.

#### Recrystallization

The recrystallization dolomites are generally represented by large-sized (a few hundreds of microns) rhomboedral to subrhomboedral crystals, which often show inclusions of much smaller rhomboedral dolomite crystals. This, together with the disappearance of any textural remain of precursor suggests successive phases of recrystallization of previous dolomitic elements (Buigues, 1982; Purser and Aïssaoui, 1985). Within a given reef complex, the oldest dolomites of recrystallization have been shown to be those having the highest Mg content, this increase in Mg/Ca ratio compared to the other dolomite types may be due to a gradual equilibration toward a stoichiometric composition, characteristic of many ancient dolomites in fossil reefs (Buigues, 1982; Berbey, 1989; Koch and Shorr, 1986).

### Distribution of dolomite in reefs

The study of diagenesis in Holocene and Pleistocene reefs constitutes a major contribution to our general understanding of dolomitization of carbonate platforms because ancient platforms have generally undergone a complex diagenetic history including several phases of dolomitization including syndimentary and burial diagenetic stages.

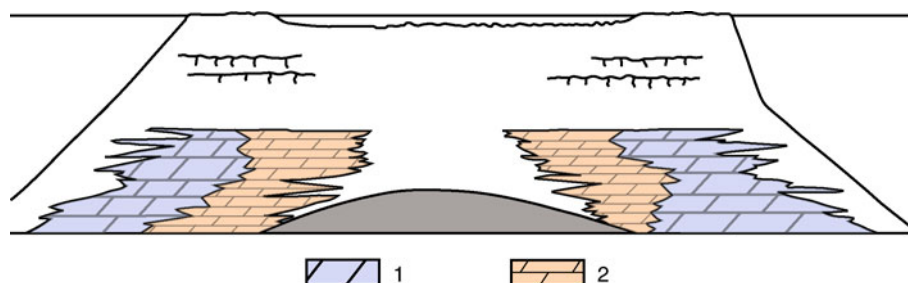
As shown in recent Cenozoic reefs, although the different types of dolomite (cementation, replacement, and recrystallization) may occur in the same reef facies, some broad general trends have been described showing the dominance of some processes in some parts of the reef complex (Figure 3). The dolomitic cements tend to dominate the external margins of the reef complex where primary porosity is higher due to coarser facies and circulation of diagenetic fluids more efficient. By contrast, the replacement dolomites are usually better developed in the lagoonal or back-reef finer sediments while the recrystallization dolomites are more characteristic of the oldest basal parts of the dolomitic body (Buigues, 1982; Aïssaoui, 1986; Purser et al., 1994).

### Dolomitizing fluids

#### Isotopic approach

The stable isotopic composition of dolomites may reveal the marine or nonmarine signature of dolomitizing fluids providing that the studied dolomites have not undergone a too complex diagenetic history. In that sense, the partially dolomitized facies frequently occurring on the top and margins of the dolomite body under modern reef platforms have been shown to be the most informative for the understanding of the modalities of dolomitization.

Although several models of dolomitization of carbonate platform have been considered, the prevalent model for explaining the dolomitization of reefs is the "mixing zone" system or Dorag model (Badiozamani, 1973), mainly deduced from the isotopic signature of dolomites suggesting a certain mixture of marine and meteoric waters (Buigues, 1982; Purser and Aïssaoui, 1985;



**Diagenesis, Figure 3** Schematic cross-section of Mururoa Atoll, showing the distribution of the various types of dolomite. (a) dolomitic cement dominant and (b) replacement dolomite dominant. (Modified from Purser et al. [1994].)

Aïssaoui et al., 1986; Buddemeier and Oberdorfer, 1986; Carrière, 1987).

#### *Petrographical and geological approach*

Although the petrographical and geochemical characteristics of dolomites in Quaternary reefs are known to be highly variable, the change from a calcium carbonate to a mixed Ca–Mg carbonate required a source of Mg ions, which is reasonably regarded as provided by the marine water. On the other hand, the fact that marine waters alone cannot produce massive dolomitization of the reef complex is evidenced by two basic petrographical observations: (1) the dolomitization is often associated with previous dissolution features linked to meteoric waters and (2) the most external parts of modern reef platform is not dolomitized (Aïssaoui, 1986).

#### **Diagenetic alteration – crystalline modifications** **Calcitization of aragonite**

The recrystallization from aragonite to calcite may concern either aragonite cements (Sandberg, 1984; Aïssaoui, 1985) or biogenic aragonites (James, 1974; Pingitore, 1976; Gvirtzman and Friedman, 1977; Sandberg, 1984; Dullo, 1986). In both cases, the transformation involves at very small scale, a prior discrete dissolution process of the aragonite precursor, followed by a precipitation of calcite within the newly created secondary voids, both processes may occur concomitantly at very short distances (a few microns to tens of microns) from each other. The overall transformation operates as a migrating front of dissolution–precipitation. While this appears obvious in the case of aragonite cement, in some biogenic aragonite the transformation may be further controlled by the textural and compositional differences of the skeletal structures, making hence the recognition of a geometrically simple front of dissolution–precipitation difficult.

These concomitant discrete processes of dissolution–precipitation strongly differ from the transformation at solid state characteristic of metamorphic conditions.

#### **Transformation of HMC to LMC**

In the cored material from Mururoa Atoll, several types of magnesian calcite cements having different Mg values

have been described (Aïssaoui and Purser, 1985; Aïssaoui, 1986). The type 2 cement has variable Mg values, always equal or lower than the type 1 cement. The type 2 cement has been interpreted as resulting from the gradual diagenetic transformation of the early marine fibrous HMC cement (Aïssaoui and Purser, 1985). In the deeper parts of the atoll rim, the early fibrous or radial calcite cements have even lower Mg values (less than 3% mol  $\text{MgCO}_3$ ) (Berbey, 1989). This gradual change of Mg content likely results from diagenetic processes involving partial micro-dissolution of HMC, as suggested by Berbey (1989), and/or Ca–Mg substitution in the calcite lattice.

#### **Dolomitization**

Dolomitization may affect either bioclots, or sediment, or early diagenetic cements, in particular HMC cements. Dolomite can replace calcite or aragonite precursors. The gradual development of dolomite to the detriment of the calcite or aragonite occurs through a migrating front of dissolution–precipitation leading to a progressive digestion of the calcite or aragonite precursor by dolomite (Gebelin et al., 1980; Aïssaoui, 1986).

#### **Skeletal diagenesis**

Skeletal carbonates, including those occurring in reef facies, are known to be highly susceptible to diagenesis and often undergo rapid and discrete diagenetic changes at a very early stage either postmortem or even already during the life of the organism. These first steps of diagenesis in skeletal carbonates are represented by discrete textural changes, micro-dissolution features and isomineral recrystallization. They have been evidenced both within biogenic aragonite (Macintyre and Reid, 1995; Perrin and Cuif, 2001; Perrin, 2004) and magnesian calcite skeletons (Macintyre and Reid, 1998; Reid and Macintyre, 1998; Hover et al., 2001). These rapid changes are strongly favored by two main features: the early degradation of intraskeletal organic matrix and the micronic size of individual biocrystals (Robbins and Ostrom, 1995; Perrin and Smith, 2007b).

## Models of reef diagenesis

Within the reef masses, hydrodynamic movements and biological activities are determinant factors controlling in various degrees and at different scales the physicochemical conditions in which diagenetic processes are operating.

### Early marine cementation

One of the most important mechanisms causing the active preferential lithification of external reef margins is the strong hydrodynamics able to displace large volumes of seawater through the reef framework from the external reef flanks to the internal zones, and hence providing significant inputs of dissolved calcium carbonate. Additionally, the textural properties of reef sediments typical from these environments, principally represented by grain-supported facies with high porosity and permeability, also favor the circulation of oceanic water through the reef mass.

The development of marine cementation is independent of climate and of the type of reef complex. As a consequence, the fact that marine cementation is more developed along the reef margin has been recognized in numerous modern reef platforms, islands, and atolls and has been also frequently observed in many fossil examples (Figure 4). This has been nicely summarized as the “principle of maximal cementation” by Aïssaoui and Purser (1985, 1986).

### Meteoric cementation

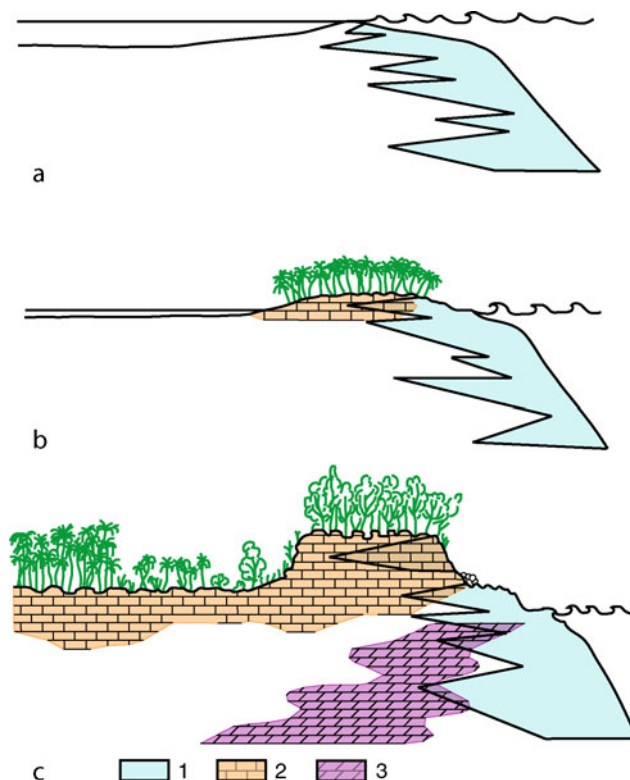
Meteoric cements in reefs are mainly dependent on two driving factors: (1) the emerged relief, which determines the extension and thickness of sediments susceptible to be affected by cementation and (2) the regional climate, which may favor the solution of important amounts of calcium carbonate and hence participates indirectly in the oversaturation of waters responsible for cement precipitation (Figure 4).

During this meteoric diagenesis, dissolution occurs contemporaneously with cementation through flooding of interstitial fluids. Therefore, the precise delimitation of the volume within which meteoric cementation takes place is difficult to determine. However, at the scale of platform or reef complex, the meteoric cementation tends to be better developed in the central/internal parts of the platform and to affect stratiform volumes (Aïssaoui and Purser, 1986; Carrière, 1987; Perrin, 1990).

### Dolomitization

In most recent and many ancient reefs, the presence of a mixing zone developed during sea-level low stands is invoked for explaining the formation of dolomititic body in reef platform. The mixing nature of dolomitizing fluids is deduced from the isotopic composition of dolomites, their trace elements content, and their petrographical patterns.

However, the presence of a mixing zone implies that the carbonate buildup was an emerged island with



**Diagenesis, Figure 4** Models of reef diagenesis with different types of reef history: (1) early marine cementation, (2) postdepositional meteoric cementation, and (3) mixing zone dolomitization. (a) subtidal reef complex, (b) emerged reef complex with low relief, (c) emerged reef complex with high relief. (From Aïssaoui [1986].)

a freshwater lense having a significant thickness at the time of dolomitization. Moreover, a centripetal movement of oceanic waters from the external reef margin to the internal parts of the platform is required to explain the supply of Mg from the ocean to the mixing zone and the genesis of the dolomite body. The preferential distribution of dolosparite cement, compared to the replacement and recrystallization forms of dolomite, in the facies from the external parts of the reef also corroborates this view of centripetal displacement of waters through the reef volume.

Several mechanisms may act independently or together responsible for producing this centripetal water movement. These are (1) the natural movements of oceanic waters such as waves, tidal currents, and storm waves; (2) thermal convection generated by the difference of water temperature between the internal parts of the platform and the ocean (Rougerie and Wauthy, 1986; Rougerie, 1995); and (3) at a larger timescale, eustatic fluctuations also produce lateral water movements.

The genesis of a dolomititic body in a reef complex is directly linked to three main conditions (Figure 4):

1. The presence of a mixing zone between marine and nonmarine waters.



2. An active hydrodynamics generating a centripetal displacement of oceanic water, which passes through the reef mass.
3. The presence of an aquifer of a minimal size necessary for the development of a significant dolomitic body. This supposes a relatively important relief above sea level or surface area of the emerged island (Aïssaoui, 1986).

### Outlook: What we still do not know about reef diagenesis

The diagenetic modification of a carbonate sediment results from cumulative effects of numerous biological, physical, and chemical processes acting independently and successively in time or interacting concomitantly. The diversity of processes involved and the way they may interact with each other leave in our present understanding of carbonate diagenesis several, if not many, important gaps and question marks, some of which are listed and briefly discussed below, but the list is far from being exhaustive.

### Role of organic matter

The interactions between organic matter and carbonate precipitation or dissolution have been invoked in numerous works on carbonate diagenesis, including reefs, since the beginning of studies of diagenesis in carbonate platforms. In particular, the influence of organic compounds is frequently considered as the potential cause of the non-thermodynamic behavior of carbonates (Morse et al., 2007).

The assessment of the complex and diverse interplays between carbonate mineral and living, dissolved or amorphous organic material has made significant progress in the past 2 decades, but is still in its infancy. Both *in vitro* experimentation and *in situ* observation-based research in natural environments are needed in order to improve our understanding of such systems.

Three different categories of interactions, which are potentially of tremendous importance for diagenesis, may be distinguished: (1) the behavior of carbonates (and related diagenetic processes) in the presence of dissolved organic matter, (2) the relationships between organic compounds and mineral surfaces via adsorption at preferential sites, and (3) the presence of glycoproteinous material as intraskeletal organic matrices within skeletal carbonates and bioclasts.

### Role of microbial processes in reef diagenesis

In recent years, research investigations on living coral reefs have been focused on the qualitative and quantitative assessment of microbial benthic communities, including photosynthetic microphytobenthos. This notably revealed that the contribution of these microbial associations to the primary carbonate production of the entire reef ecosystem may be in the same order of magnitude of the production estimated for corals (Werner et al., 2008). The potential

role of these microbes on the processes of early diagenesis, especially marine cementation, has to be investigated together with the general understanding of possible interactions between single microbes, biofilms, and mineral surfaces in marine and nonmarine interstitial waters.

Inversely, the role that early diagenesis can play in the preservation of these biofilms and traces of microbial assemblages in recent and deep geological record appears particularly complex and represents a still open field for future research.

As far as reefs and carbonate platforms are concerned, these two points have strong and direct links with the practical highly relevant questions of the origin and interpretation of peloids (their nature as cement, internal sediment, or microbialite) and the general lack of discriminant criteria for inferring the nature of micritic crusts in general.

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## Cross-references

[Antecedent Platforms](#)  
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## DOLOMITIZATION

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### Definition

Dolomite,  $\text{CaCO}_3 \cdot \text{MgCO}_3$ , is a common *mineral*, usually found with limestone ( $\text{CaCO}_3$ ). The *rock*, consisting principally of the mineral dolomite, is also called dolomite; more recently it has come to be called dolostone. The process of the formation of the mineral and rock is referred to as dolomitization.

### Dolomite, the mineral, and the dolomitization process

Dolomite, the mineral, was named at the end of the eighteenth century by the French Naturalist/Geologist Deodat Gratel de Dolomieu (1750–1801) for rocks in the Southern Tyrol Alps of northern Italy, an area now referred to as the Dolomites. The study of the formation of dolomite commenced with the classic papers of Cullis (1904), Skeats (1905) and Van Tuyl (1916). The reader is referred to Deelman (2008) for a comprehensive discussion on its mineralogy, regional occurrences, mechanisms of formation, and the subtleties of its chemistry including ordered/disordered and stoichiometric/enriched dolomites. Dolomite is not a solid solution series with Ca and Mg end members but a mixed lattice crystal, which contains approximately equal amounts of  $\text{CaCO}_3$  and  $\text{MgCO}_3$ . The  $\text{Ca}^{2+}$  and the  $\text{Mg}^{2+}$  ions are separated into individual monolayers, which are themselves separated by carbonate ion layers. Simple substitution of calcium ions by magnesium ions is not possible and non-stoichiometry is very common. Usually, the wt%  $\text{CaO}$ :wt%  $\text{MgO}$  = 3:2. This is a very important factor to be considered in the models of dolomitization, for simple substitution of  $\text{Ca}^{2+}$  ions by  $\text{Mg}^{2+}$  ions is not chemically feasible and dolomitization models that propose this process are in error. Notwithstanding this, seawater is an ideal source of the  $\text{Mg}^{2+}$  ions for dolomitization in reefal carbonates. Nucleation of dolomite cannot be explained in terms of classical equilibrium thermodynamics. Deelman (2008) proposes that reaction kinetics that provide ongoing multiple fluctuations better explain dolomite formation. "The kinetic hindrances to dolomite precipitation from seawater can be overcome by evaporating seawater, diluting it, raising the temperature or lowering the  $\text{SO}_4^{2-}$  content" (Tucker and Wright, 1990). These authors as well as Deelman (2008) provide a comprehensive, up-to-date account of the complexities of dolomite formation, either as a primary precipitate or as a secondary replacement of a metastable precursor mineral. It was Deelman (1999) who first explained how dolomite can form under low temperatures and atmospheric conditions through



alternating conditions of dissolution and precipitation whereby metastable precursor minerals, such as magnesium calcite, change to more stable phases such as dolomite. Such conditions require large-scale fluctuations in pH, which is controlled by the  $p\text{CO}_2$ . Deelman has explained how “breaking Ostwald’s Rule,” which governs the course of irreversible geochemical reactions, can occur when fluctuations of sufficient amplitude, frequency, and duration are capable of crossing the border between metastable and stable fields, and both metastable and stable phases will nucleate simultaneously. During these fluctuations, conditions opposing the subsequent growth of the metastable phase will favor continued growth of the stable phase. This explanation gets around one aspect of the Dolomite Problem (Fairbridge, 1957; Hsu, 1966; Land, 1985, 1998; Hardie, 1987; Fowles, 1991; Braithwaite, 1991), which centers around the observation that dolomite will not precipitate from normal or oversaturated solutions at low temperature and atmospheric pressure. The second part of the paradox is that dolomite is a very common carbonate mineral in sedimentary rocks throughout the geological record, which contrasts with the relatively limited amount of modern day surface dolomite (see Wright and Wacey, 2004). Clearly, there has to be a simple explanation of the process of dolomitization.

Vasconcelos et al. (1995), Vasconcelos and McKenzie (1997), and McKenzie and Vasconcelos (2009) have proposed that microbial mediation may overcome the thermodynamic and kinetic barriers to dolomite nucleation in the natural environment. Anaerobic bacteria can play a role in primary dolomite precipitation and secondary replacement (Warthmann et al., 2000). Clearly, the presence of microbes is the indispensable component driving the reaction.

### Dolomite occurrences and hydrological processes

Deelman (2008, Chapter 4) provides a comprehensive account of the regional occurrences of Recent dolomites. In addition to the occurrences in coral reefs, atolls, and guyots which are discussed later, dolomite is forming in the Coorong region of South Australia, in deep sea sediments with high organic content (organogenic dolomite), in the carbonate platforms of the Bahamas, in the hot arid sabkha environments, especially, in the Middle East and in the supersaturated saline lagoons along the Rio de Janeiro coast of Brazil, namely, Lagoa Vermelha and Brejo do Espinho. Clearly all these environments, irrespective of their unique hydrological circumstances, are characterized by physiochemical conditions that fluctuate “wildly” in the presence of enhanced microbial activity. The hydrological setting in which dolomite is known to be forming have been summarized into the following: seepage reflux, capillary concentration, evaporative pumping or sabkha, solution cannibalization, groundwater-seawater mixing, Dorag dolomitization, geothermal springs, storm

recharge, Kohout convection, tidal pumping, coastal zone mixing, and evaporative mixed water. In all of these settings, seawater in some form of modification flows through the sediments or sedimentary rocks allowing for both primary deposition and replacement of preexisting carbonate particles. Often the resultant dolostone preserves the original depositional textures and “ghosts” of preexisting grains. Tucker and Wright (1991) provide a comprehensive account with numerous illustrations of these hydrological settings where dolomite is forming present day.

### Dolomite in reefs, atolls, and guyots

Montaggioni and Braithwaite (2009) provide a very useful summary of the occurrence of dolomite in Quaternary coral reef. The best data on dolomitization comes from the deep drillings of the Pacific and Indonesian atolls, especially, Enewetak, Mururoa, and Midway, all of these having been drilled more than once to pre-reefal basement.

The earliest account of the occurrence of dolomite in coral reefs is that of Skeats (1903) and Cullis (1904) in the cores recovered from the 1896 drilling undertaken by the Royal Society of London at Funafuti Atoll. Here, dolomite crystals were only detected at depths greater than 194 m where dolomite became the predominant carbonate mineral. Other drillings of Pacific Atolls (Skeats, 1905) also recorded the occurrence or the absence of dolomite (Deelman, 2008). Of particular significance were the drillings at Niue (Wheeler and Aharon, 1997; Aharon et al., 1987), Kita-daito-jima (Suzuki et al., 2005), Bikini (Ladd et al., 1948), Enewetak (Saller, 1984), Midway (Ladd et al., 1970), Mururoa and Fangataufa (Aissaoui et al., 1986; Aissaoui, 1988).

Fairbridge (1950) commented on the fact that drillings at Bikini, Maratoca (Indonesia), and the Great Barrier Reef bores of Michaelmas Cay and Heron Island did not encounter dolomite. He inferred that anoxic conditions were not present to facilitate dolomitization. More recent drillings of the Guyots of the Mid-Pacific Mountains and western Pacific have recorded the occurrence of dolomite (Flood, 1998). Recent drilling of Boulder Reef and Ribbon Reef No. 5 of the Great Barrier Reef (International Consortium for Great Barrier Reef Drilling, 2001; Webster and Davies, 2003; Braithwaite et al., 2004) failed to record the presence of dolomite, whereas deep drillings on the Queensland Continental Slope (Swart, 1993) did record the presence of dolomite.

In the Enewetak Atoll bore, Ladd et al. (1953) could not discern any pattern in the distribution of dolomite. It only occurred at depths below 1,340 m, whereas in the Kita-daito-jima bore dolomite was found only in the upper 122 m. On Midway Atoll, dolomite was found between 130 and 150 m depth. This variability in depth of the dolomite occurrences would suggest that there is no relationship between dolomite formation and water depth. Schlanger (1963) reexamined the cores from the atolls of

Funifuti, Kita-daito-jima, and Enewetak and made several deductions concerning dolomite formation. Clearly, dolomite formation was not a function of depth. No relationship between its occurrence and duration of immersion in seawater could be established. There was no obvious relationship between the presence of porosity and the occurrence of dolomite. He stated that "each atoll displays a unique pattern of distribution of dolomite." In the borings at Mururoa Atoll, Aissaoui et al. (1986) have demonstrated an extensive thickness of dolomite where the dolomite attains maximum thickness at the periphery of the atoll and thins toward the former volcanic edifice (Bardintzell et al., 1985). Trichet et al. (1984) have described in great detail the dolomite occurrences and the hydrological model responsible for the dolomitization which essentially involves dissolution – precipitation processes (Aissaoui et al., 1986; Aissaoui, 1988). The dolomite occurrences at Niue have been comprehensively documented by Aharon et al. (1987) and Wheeler and Aharon (1997) who report that the dolomite is "generally limited to two vertically distinct units which are separated by a 120 m thick interval of undolomitized limestone." They proposed that in the upper dolomite layer tidal pumping through the more permeable layers could have produced the tabular bodies of dolomite, whereas in the lower dolomite unit it is more likely to have been produced from ocean-derived saline groundwater flow and reheating.

In Resolution, Wodejebato and MIT guyots of the northern and northwestern Pacific Ocean where drilling was conducted in 1992 (Ocean Drilling Program, Legs 143 and 144) dolomite was recorded at considerable depth in excess of 2,000 m (Flood, 1998; Flood and Chivas, 1995; Flood et al., 1996). In hole ODP 866A on Resolution Guyot, the dolomite rock preserves the original depositional texture and also exhibits ghosts of the preexisting carbonate grains. The isotopic composition of the dolomite display oxygen, carbon, and strontium values indicative of precipitation from slightly modified seawaters. Here two distinct dolostone units occur; one is brown in color with a sugar-like texture, and the other is white with a massive crystalline appearance. The former appears to have formed slightly after deposition of the carbonate sediments whereas the second pulse of dolomitization responsible for the massive white dolomite occurred some 100 million years after the depositional age of the enclosing carbonates.

There are many other reported occurrences of dolomite in reefs, but they are too many to record herein. However, some will be mentioned to direct the reader to the extensive literature. They are Mitchell et al. (1987), who have described modern marine dolomite cement in a north Jamaican fringing reef; Strasser and Strohmenger, (1997) who have described dolomite occurrences in the Pleistocene reefs of the Southern Sinai, Egypt; Shinn et al. (1965) and Vahrenkamp and Swart (1994), who have reported upon Recent supratidal dolomite from Andros Island, Bahamas; and Bourrouilh (1973), Chevalier

(1973), and Coudray (1971), who have described dolomite in modern reef environments in New Caledonia.

## Summary

Dolomite,  $\text{CaCO}_3 \cdot \text{MgCO}_3$ , is a mineral commonly found with limestone and carbonate sediments of coral reefs. Dolomite does not precipitate from normal seawater or solutions at low temperature and atmospheric pressure, yet it is a very common carbonate mineral in sedimentary rocks throughout the geological record. This paradox is referred to as the Dolomite problem. Dolomite is not a product of a  $\text{CaCO}_3$ - $\text{MgCO}_3$  solid solution series but it is a mixed lattice crystal whose nucleation cannot be explained in terms of classical (equilibrium) thermodynamics where Ostwald's step rule governs the course of irreversible geochemical reactions. It was as recently as 1999 that Deelman suggested that Ostwald's Rule can be broken when fluctuations of sufficient amplitude, frequency, and duration occur and they involve changes in pH conditions related to variable  $\text{pCO}_2$ . Under such conditions a metastable precursor to dolomite (such as magnesium calcite) forms and through repeated alternations of dissolution and precipitation, change to more stable phases (such as magnesite or dolomite). He proposes that such fluctuations allow for both the metastable and stable phases to nucleate simultaneously and that during such fluctuations, conditions opposing the subsequent growth of the metastable phase will favor continued growth of the stable phase. It has recently been suggested by other researchers that the presence of microbial mediation could overcome the thermodynamic and kinetic barriers to dolomite nucleation in the natural environment.

The majority of hydrological settings in which dolomite is known to occur involve special conditions which are characteristically highly variable and fluctuating and are dominated by enhancement of fluid flow, usually of modified seawater through preexisting carbonate sediments and sedimentary rocks, especially coral reefs.

The occurrences of dolomite in Modern coral reefs and atolls has been known for over 100 years, yet the process of dolomite nucleation has evaded adequate chemical explanation until 1999 when Deelman proposed a way that it could happen. The deep borings of the Pacific Ocean Atolls and Guyots have provided a window to view the occurrence of dolomite and the processes of its formation. Of special significance have been the results of scientific investigation at Funafuti Atoll, Enewetak Atoll, Midway Atoll, Niue, Kita-daito-jima Atoll, Mururoa Atoll, Fangataufa Atoll, Christmas Island and Resolution Guyot, Wodejebato Guyot, and MIT Guyot. Equally important have been those deep borings where dolomite was not reported. They include the Great Barrier Reef, Bikini Atoll, Makatea Island, Guam Island, to name just a few. No discernable pattern of dolomite occurrence could be established. The overarching dolomitization

process in all the hydrological models involves seawater, somehow modified, and dissolution – precipitation associated with repeated fluctuations such as tidal pumping, wave action, deep ocean currents, sea-level oscillations, pulses of thermally elevated water flow, etc. The process of dolomite formation may be penecontemporaneous with sedimentation but it is more frequently postdepositional, even diagenetic. Sometimes, there can be a considerable time delay of the order of 100 m.a. between sedimentation and dolomite formation.

The more recent realization that anaerobic bacteria can play a role in the primary precipitation of dolomite is an avenue for fruitful research in addressing the topic of dolomite formation and occurrence.

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## Cross-references

[Atolls](#)

[Coral Reef, Definition](#)

[Diagenesis](#)

[Porosity Variability in Limestone Sequences](#)

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## DOUBLE AND TRIPLE REEF FRONTS

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## Definition

The reef front is the windward margin of a coral reef with multiple fronts produced by narrower and younger sections of reef flat to windward of the main front.

The windward side of most reefs is formed by a straight edge or “hard line.” Occasionally, however, there may be a second or third line of reefs separated from the main reef by linear lagoons up to 300 m wide and 10–30 m deep. Such features have been described in New Caledonia (Guilcher, 1965; Chevalier, 1973; Battistini et al., 1975), Mayotte (Battistini et al., 1975), and Australia’s Great Barrier Reef (Hopley et al., 2007). It is suspected that other reefs, especially shelf reef systems may contain similar features.

Where double barriers occur, the outer reef invariably appears younger and may be still slightly submerged (see for example the double barrier of S.E. New Caledonia shown in Figure 5, Battistini et al., 1975). This has resulted in the suggestion that the outer barrier(s) grew from deeper foundations possibly added to the reef front as terraces during the last glacial interstadials or the Holocene transgression. The examples of the Great Barrier Reef suggest that such terraces are typically at 20–30 m depth while the Pleistocene reef to which they are attached is only 10–15 m below modern sea level. Contrasting rates of growth may have resulted: the reef growing from the terrace lagging behind sea level rises as a “catch up” reef while the main reef growing from the more extensive Pleistocene foundations would have adopted a “keep up” strategy, the result leading to a mature reef (crescentic, lagoonal) and an immature secondary reef front.

The double reef front on Gable Reef (20° 48' S) (Figure 1) has been examined in detail (Hopley et al., 2007, Figure 8.13). This Great Barrier Reef site is on the windward south-eastern rim with the secondary rim stretching partly across a wide embayment. The depth of



**Double and Triple Reef Fronts, Figure 1** The massive second front on Gable Reef overlying a reef front barrier or spit deposited during the Holocene transgression (see Hopley et al., 2007 Figure 8.13). Dating suggests that the main reef adopted a “keep up” mode during the Holocene transgression reaching modern sea level about 6 ka while the second front was a “catch up” reef 500–600 years behind its main counterpart. (courtesy Cambridge University Press)

the intervening lagoon is 20–25 m. One hole drilled into the outer rim reached 30 m but did not penetrate the Pleistocene. However, seismic survey suggested that it was 25–30 m beneath the lagoon and second front and ca. 20 m beneath the main reef. Surprisingly, the double front may not be a classic example as drilling showed that below ca. 12 m it was mainly sand suggesting that the foundations were provided by a sand barrier or spit across the embayment, as also suggested by the morphology.

Gable Reef’s main reef flat has an age of 6–5 ka, while the age of the secondary reef flat is <1.3 ka. However, only 5 m below the surface it is >5.5 ka and appears to have lagged behind the main rim by only 500–600 years. Although more complex than double fronts growing from reef terraces, the Gable Reef example does provide insight into the growth rates and age relationships of similar features elsewhere.

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## Cross-references

[Coral Cay Classification and Evolution](#)  
[Fore Reef/Reef Front](#)  
[Reef Classification, Response to Sea Level Rise](#)  
[Submerged Reefs](#)

# E

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## EARTHQUAKES AND EMERGENCE OR SUBMERGENCE OF CORAL REEFS

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### Synonyms

Coseismic displacement of coral reefs; Coseismic emergence or submergence of coral reefs

### Definition

Earthquakes and emergence or submergence of coral reefs: refers to vertical tectonic displacement of coral reefs associated with an earthquake. Coseismic vertical motion may cause submergence or raise the shallow part of reefs to levels relative to sea level above where they can live. The amount of vertical motion may be barely detectable or can exceed 10 m. Subsidence is less obvious than uplift, but both provide significant information regarding earthquakes and tectonic processes.

### Introduction

Early geologists realized that crustal uplift and subsidence as well as sea-level changes helped to create atolls and barrier reefs and emplace fossil coral reefs at elevations from slightly above to hundreds of meters above sea level (e.g., Darwin, 1842; Guppy, 1887; Dana, 1890). However, the relationship to earthquakes, and the causes, frequency, rates, and amounts of vertical movement for each event were matters of conjecture until examples of coseismic reef uplift were described in scientific reports (e.g., Figure 1; Taylor et al., 2008). Today, we know that both coseismic and aseismic mechanisms cause vertical displacement, but coseismic movement is nearly

instantaneous and much more dramatic. In extreme cases, uplift may be as great as ~20 m. Coseismic uplift is generally easier to recognize and document than subsidence because it causes emergence and mortality of coral and other organisms raised higher than their highest level of survival (HLS) (Taylor et al., 1987).

Coseismic reef uplift and subsidence have been documented in two geologic settings: (1) Near volcanoes along plate boundaries or intraplate hot spots where processes such as magma chamber inflation induce motion on faults, earthquakes, and vertical motion (e.g., Newhall and Dzurizin, 1988; Kaizuka, 1992; Geist et al., 1994; Amelung et al., 2000) and (2) compressional tectonic settings along plate boundaries where vertical surface displacement commonly accompanies fault rupture. Emerged coral reefs also occur on restraining bends along the trace of strike-slip plate boundaries as along the North American-Caribbean plate boundary zone in Haiti (e.g., Dodge et al., 1983; Mann et al., 1995). Just before final submission of this manuscript significant reef uplift associated with a January 2010 earthquake along a strike-slip fault in southern Haiti has been reported (personal communication, Roger Bilham). This may be the first documented case of coseismic reef uplift along a strike-slip fault system.

Today, coral reef emergence and submergence often are measured and used to investigate aspects of the subduction process. The vertical displacements of coral reefs record the amounts and distribution of elastic strain accumulation and its release as coseismic and aseismic slip. Measurements of vertical motions provide direct information about the mechanical processes accompanying volcanism and fault slip.

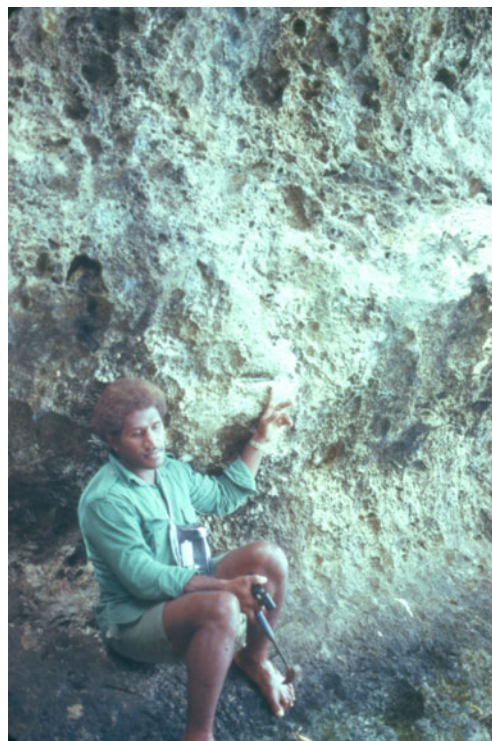
### Mysterious origin of emerged and submerged coral reefs

Geologists have long been intrigued by the mysterious origins of atolls and emerged coral reefs and debated the





**Earthquakes and Emergence or Submergence of Coral Reefs, Figure 1** *Porites* sp. coral heads along the southern coast of Ranongga Island, Western Solomon Islands, were killed by up to ~2.46 m of uplift associated with a  $M_w$  8.1 earthquake on 1 April 2007. Systematic measurements documented the geographic extent and amounts of uplift and subsidence (Taylor et al., 2008).



**Earthquakes and Emergence or Submergence of Coral Reefs, Figure 2** The mark pointed to by the seismological observer Bobby Kelly was emplaced by H.B. Guppy on 11 October 1882 on Uki-ni-Masi Island, Solomon Islands, to be used as a reference mark in case of future vertical displacement (Guppy, 1887).

causes for the large changes in relative sea level implied by their observations. Charles Darwin experienced an earthquake that caused coseismic uplift along the coast of Chile (Darwin, 1909, p. 314) and understood that coseismic vertical motions could cause coral reef emergence and submergence as well. Darwin summarized reports of emerged reefs, the likelihood that some uplift was recent, and the probable relationship of uplift to earthquakes (Darwin, 1842). However, he cited no confirmed evidence of coseismic reef uplift or subsidence. After visiting the Solomon Islands, Guppy (1887, p. 126) stated that “The different stages in the upheaval of several of the calcareous islands are clearly shown in the ledges or terraces displayed in their profiles. Such ledges indicate long intervals or pauses in the movement of elevation, during which the coral reefs by their outward extension formed reef flats, which have ultimately been to some degree preserved in the existing ledges, now raised to elevations often of some hundreds of feet above the sea.” However, based on his observations of apparently very young emerged reefs and bio-erosion notches in the Solomon Islands, Guppy (1887, p. 128) concluded that “. . . the protracted elevatory movements of one or two hundred feet and over have consisted in a succession of small upheavals of perhaps not more than five or six feet at a time.” To provide a basis for future measurements of vertical change he emplaced “datum” marks at several locations in the Solomon Islands. One of his marks on Uki-ni-Masi Island was located 5 ft. above high-water spring tide on 11 October 1882. During a visit on 29 July 1986, we found the mark at 5 ft 5 in. above high tide of that day and thus of no discernible difference in elevation than when installed by Guppy (Figure 2).

The earliest credible accounts of coseismic reef uplift came from missionaries and administrators and generally contain virtually no geological description or mention of uplifted corals. An example is the reported ~6 m volcanogenic coseismic uplift of a reef near Yasur Volcano on Tanna Island, New Hebrides (now Vanuatu) on 10 January 1878 followed by a few meters more uplift about a month later (Lawrie, 1898). Another account indicates that the second uplift occurred ten years after the first (Mawson, 1905). Both reports were based on second-hand accounts from missionaries. Another second-hand report of coseismic reef vertical movements comes from San Cristobal Island (Makira Island), Solomon Islands, associated with a large earthquake sequence in October 1931 (Gold, 1932; Grover, 1958). However, again these reports provided no details regarding amounts of reef emergence or subsidence and no more than a vague indication of its geographic extent.

### Scientific reports of coseismically displaced coral reefs

Perhaps the earliest first-hand scientific report described coral uplift on Malakula Island, Vanuatu, associated with a  $M_w$  ~7.7 subduction zone earthquake on 11 August 1965 (Benoit and Dubois, 1971), but the authors visited

the site several years after the event. Later, Taylor et al. (1980, 1987) mapped the uplift with hundreds of systematic measurements of emerged corals and used the data to analyze seismic slip. Maximum uplift for the 1965 event as measured in 1976 was  $\sim 1.2$  m. Additional coseismic uplift of Northern Malakula reefs occurred in association with a July 1994 earthquake south of Malakula Island (Calmant et al., 1999). Also, Pelletier et al. (2000) measured uplift of Ambrym Island, Vanuatu, near a back-arc reverse-fault earthquake in 1999.

In some cases, maximum coseismic reef uplift or subsidence may be only a few centimeters or less, as discovered by Pandolfi et al. (1994) following a May 1992  $M \sim 7.2$  earthquake along the northeast coast of Papua New Guinea. Other scientific reports of coseismic reef uplift include the Caribbean coast of Costa Rica (Plafker and Ward, 1992) and the Solomon Islands (Taylor et al., 2008). However, the most spectacular reports of coseismic reef uplift are for the great  $M_w \sim 9.1$  26 December 2004 Sumatra-Andaman earthquake that ruptured from northern Sumatra northward past the Andaman and Nicobar Islands producing uplift up to 1.5 m on some islands (Bilham et al., 2005; Meltzner et al., 2006; Rajendran et al., 2007). Subsequently on 28 March 2005, an adjacent area of the forearc ruptured beneath Nias Island causing uplift as great as 3 m, but over a smaller area (Briggs et al., 2006).

Informed by the historical reports of volcanogenic coseismic uplifts near Yasur Volcano (Lawrie, 1898; Mawson, 1905) on Tanna Island, Vanuatu, Chen et al. (1995) measured a combined uplift of  $\sim 20$  m based on well-preserved branching corals and heads on the forest floor. Uranium-series and radiocarbon dating confirmed that the corals died  $\sim 1878$  A.D. and documented several previous uplifts that sum to  $\sim 160$  m cumulatively over the past  $\sim 1,100$  years, possibly related to magma chamber inflation. Most if not all of this uplift was confined to the Yenkahe horst area and is not detectable elsewhere on Tanna Island.

Earthquakes may have accompanied uplift of coastal volcanic Mount Suribachi on Iwo Jima (Newhall et al., 1998) and  $\sim 6$  m of 1954 uplift of Urvina Bay, on the volcanic Isabela Island, Galapagos (Couffer, 1956; Colgan and Malmquist, 1987) may have been accompanied by earthquakes. A  $M \sim 6.5$  earthquake occurred on 4 June 1954 near Urvina Bay (Geist et al., 1994). Even apparently aseismic uplift of volcanic islands is often accompanied by at least small earthquakes as at Iwo Jima (Ukawa et al., 1998).

### Scientific significance of coseismically emerged coral reefs

Measurements of the amount and geography of coastal uplift and subsidence associated with the great 1960 Chile and 1964 Alaska earthquakes (e.g., Plafker, 1965; Plafker and Savage, 1970) demonstrated that vertical displacement could provide critical information about subduction processes at convergent plate boundaries. Subsequently, several coseismic reef uplifts have been used to investigate the physical parameters of earthquake faulting.

The amounts and timing of recent and ancient coral reef emergence or submergence events in both volcanic settings and near potentially active faults provides a basis for forecasting the probability of future events (e.g., Sieh et al., 2008). Volcanically related coseismic uplifts may serve as a measure of subsurface volcanic activity such as magma chamber inflation and help scientists to understand the deformation processes affecting volcanic edifices (e.g., Geist et al., 1994; Amelung et al., 2000).

Most reported coseismic vertical reef displacements have occurred in association with thrust-type earthquakes in subduction zones, usually on the main interplate megathrust or decollement. However, the 1992 coseismic uplift of part of the Huon Peninsula reef occurred where the Australian continent has collided with an island arc and probably occurred on a fault developed to accommodate collision deformation rather than being on the interplate megathrust. The 1999 coseismic uplift of the eastern part of Ambrym Island in Vanuatu was related to a  $M_w$  7.5 event on a steeply dipping backthrust reverse fault accommodating eastward displacement of several segments of the central Vanuatu arc system (Pelletier et al., 2000; Regnier et al., 2003).

Crustal displacement associated with seismic fault rupture represents the release of elastic energy stored in the lithosphere that accumulated during the interseismic period preceding the earthquake. Rupture of most convergent margin faults typically involves both horizontal and vertical coseismic displacements that are greatest overlying and adjacent to the fault, but also extending many tens of kilometers beyond the rupture zone. The amount and geographic distribution of vertical displacement may enable mapping of the rupture zone geometry and an assessment of the nature of interplate slip along the megathrust (e.g., Plafker and Savage, 1970; Taylor et al., 1987; Sieh et al., 1999; Briggs et al., 2006; Chlieh et al., 2007; Sieh et al., 2008). Scientists used corals and shorelines to document the geographic pattern of subsidence and uplift as great as 1.5–2 m following the great  $M_w \sim 9.1$  26 December 2004 Aceh earthquake (Bilham et al., 2005; Meltzner et al., 2006; Subarya et al., 2006; Rajendran et al., 2007). The measurements of uplift and subsidence constrained the temporal and spatial extent of the earthquake rupture geometry and processes (Subarya et al., 2006).

Where elastic strain release on a thrust fault or megathrust culminates in coseismic uplift and subsidence of the forearc, one can assume that the event represents only one stage in the greater long-term earthquake cycle of repeated elastic strain accumulation and coseismic release (e.g., Plafker and Savage, 1970; Savage, 1983; Sieh et al., 2008). Elastic strain typically accumulates for tens or even thousands of years prior to coseismic rupture; while strain accumulates there is slow subsidence over the locked part of a thrust fault zone, opposite to the direction of coseismic uplift (e.g., Savage, 1983). Thus, an area of coseismic coral reef uplift is likely to become an area of interseismic coral reef subsidence. If the system was



purely elastic, then over the entire cycle, the coseismic deformation would remove all of the elastic deformation accumulated during the interseismic period. However, in reality, this seldom is the case because usually there is some long-term permanent tectonic deformation over the course of an earthquake cycle (e.g., Taylor et al., 1987; Briggs et al., 2008).

### Methods to measure coseismic coral reef emergence

Precise systematic measurements of uplift, as well as subsidence, should be conducted soon after reefs are affected by earthquakes. Immediately following coseismic displacement post-seismic visco-elastic adjustments often rapidly modify the original coseismic deformation pattern. If one can measure the geography of coseismic vertical deformation soon after an earthquake, then later measurements may reveal the geographic pattern and rates of post-seismic vertical deformation.

Measurements of coseismic uplift and subsidence typically are based on the heights of corals killed by emergence relative to mean low-water (tide) level, or some other datum related to their normal shallowest depth. Taylor et al. (1987) called the shallowest level that a coral could live and grow as its “highest level of survival (HLS),” a term since adopted by other workers (e.g., Zachariasen et al., 1999; Meltzner et al., 2006).

Although other reef organisms such as coralline algae also can be used to measure uplift (e.g., Pelletier et al., 2000), corals are believed to define emergence to within a few cm (e.g., Briggs et al., 2006). Taylor et al. (1980) initiated the practice of measuring the height of numerous emerged corals of a given species relative to nearby still-living corals of the same species, thus obviating the need to establish a tidal datum for each measurement locality. The HLS for head coral genera such as *Porites* and *Goniastrea* have different relationships to sea level so that comparing the height of one genus or species to another would be likely to introduce errors. An inexpensive auto level, tripod, and rod enable quite precise measurements between numerous living and emerged corals.

In a few cases, GPS survey marks have been emplaced prior to coseismic reef displacement and then re-measured after an event (e.g., Subarya et al., 2006). The precision for GPS measurements of vertical displacement is on the order of 2 cm. A limitation of GPS is that few points have been measured and even when many more exist, coral methods probably will remain important for areas where there are no GPS measurements.

Meltzner et al. (2006) used satellite observations to estimate vertical reef displacements by observing the pinkish to red false color on ASTER, QuickBird, and other satellite images of the December 2004 Sumatra-Andamans event. These colors indicate emerged coral overgrown by algae, which occurs within days after a coral dies from emergence. They compared pre- and post-seismic images and used a tide model to estimate the tide levels at the time when each

photograph was taken. Several studies have used before and after Synthetic Aperture Radar (SAR) satellite images to estimate the amounts of coseismic vertical displacement (e.g., Tobita et al., 2006; Lubis and Isezaki, 2008).

Fieldwork in the Mentawai Islands off Sumatra has led to refinement of techniques and the term “coral geodesy” or “paleo-geodesy” to describe the use of corals to document past vertical tectonic motions (Zachariasen et al., 1999, 2000; Sieh et al., 1999; Briggs et al., 2006; Meltzner et al., 2006; Natawidjaja et al., 2006, 2007; Sieh et al., 2008). Micro atolls can record the details of coseismic and interseismic vertical motions over many decades. Annual density bands within coral heads can reveal the timing of relative sea-level changes and the absolute age can be determined using Uranium-series dates (Figure 4).

### Recognition of coseismically emerged reefs

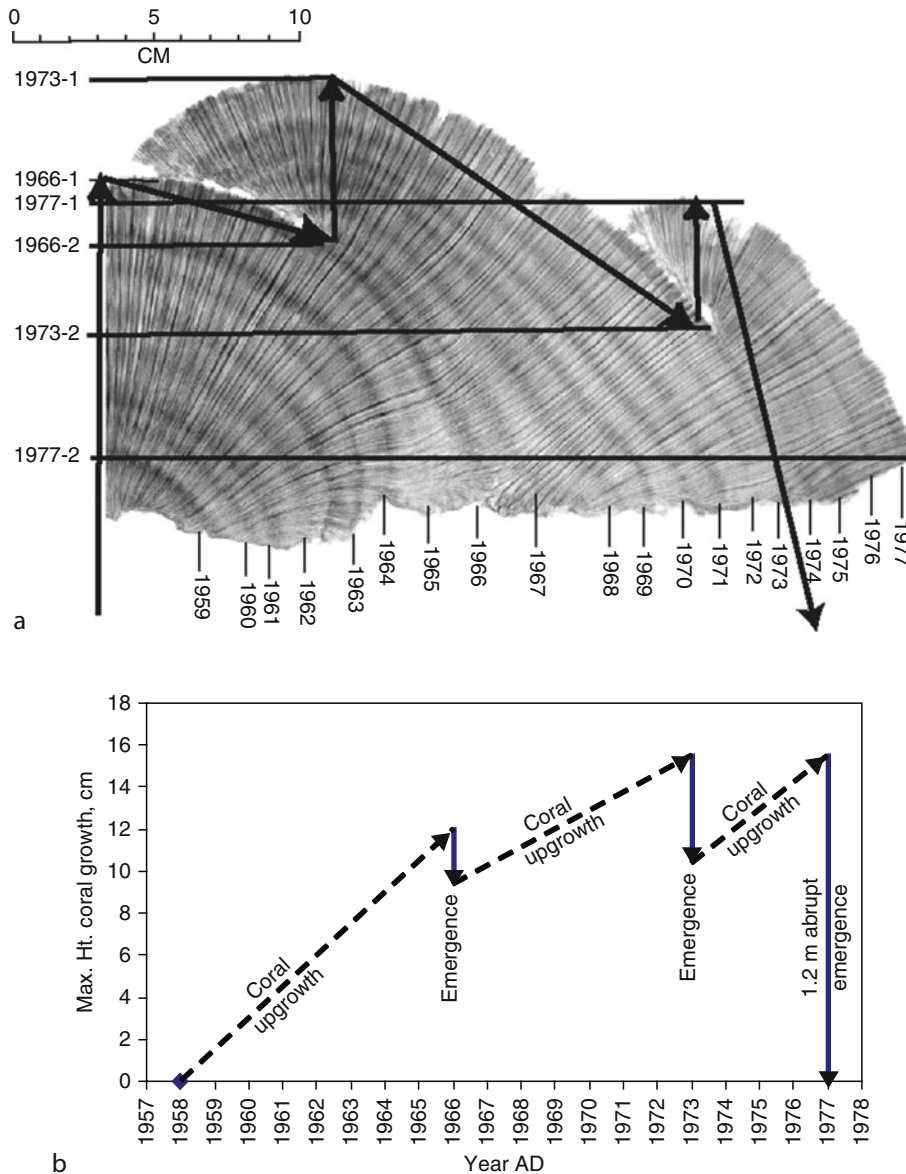
Scientists are unlikely to actually witness coseismic vertical displacement and thus the coseismic relationship to displacements generally depends on the testimony of witnesses. However, local observers may not notice small vertical movements or they may have occurred in the past when there was no oral or written record of the uplift or an earthquake. The presence of well-preserved emerged corals (Figure 3) and teleseismic or historical records of earthquakes can provide strong evidence that vertical deformation was coseismic even if living witnesses did not notice it.

After uplift, erosion and degradation of the coral record commence immediately. This can be particularly severe for corals not uplifted above the intertidal zone where bioerosion is most intense. If uplifted corals remain well preserved for hundreds of years (e.g., Fig. 3), it is



**Earthquakes and Emergence or Submergence of Coral Reefs, Figure 3** Coral head that died ~1729 A. D. is now 2.3 m ALC. This coral is 1.1 m higher than coral that was subsequently uplifted about 1.2 m on 11 August 1965. Good preservation of the coral surface indicates that it initially emerged well above high tide level and can thus be inferred to be coseismically uplifted.





**Earthquakes and Emergence or Submergence of Coral Reefs, Figure 4** (a) X-radiograph of a coral head from the south coast of Guadalcanal, Solomon Islands, showing its annual bands. This coral records a series of relative sea level changes that may or may not be tectonic except for a final uplift of more than 1 m during a sequence of large earthquakes in 1977 that completely emerged and killed the coral. The labels with numbers and years track the sequence of relative sea-level changes that affected the coral. (b) Graph showing the relative sea-level changes that the coral head underwent with time control from the coral's annual banding.

sometimes possible to infer that a prehistoric earthquake caused uplift. On Malakula Island, Vanuatu, we find corals that were uplifted about 1.2 m in 1965. A  $\sim 1.2$  m higher than the 1965 corals are older corals that were uplifted during a previous event in about A.D.1729 (Taylor et al., 1990). The preservation of these higher-level corals is evidence that the uplift that killed them was about  $\sim 1$  m. Had the initial uplift been only  $\sim 0.5$  m, then the corals would have been submerged during high tides and would have been exposed to severe bioerosion.

### Determining the ages of vertical displacements recorded by corals

Several dating methods may be used to constrain the timing of coral emergence. If partially emerged coral heads are still living, annual density growth bands may be revealed by X-radiographs of a slab and the timing of emergence events can be determined by counting annual density bands inward from the living surface (e.g., Taylor et al., 1987; Buddemeier and Taylor, 1998) (Figure 4). If a coral is completely dead then it may be dated by

radiocarbon or by  $^{230}\text{Th}/^{234}\text{U}$ , a method precise to about 1% of the age (e.g., Edwards et al., 1989; Shen et al., 2008). Combining  $^{230}\text{Th}$  and density band counting can date multiple relative sea-level changes recorded within a dead coral head that is hundreds or even thousands of years old (e.g., Zachariasen et al., 1999).

## Summary/outlook

Methods to document and measure coral reef emergence and submergence are now well developed and comprise an important contribution to the understanding of earthquake rupture and the subduction process. Coral micro atolls record the details of both uplift and subsidence over recent centuries or even millennia. Space-based GPS and radar methods have greatly improved the temporal resolution of measurements and can measure horizontal strain as well as vertical motions. With numerous scientists aware of the scientific value of coseismically emerged and submerged coral reefs, it is likely that most future large events will be measured adequately. Smaller ones are not likely to be recognized and investigated unless they occur in an area that is easily accessible or are located in an area of particular scientific interest where GPS survey marks already exist.

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## Cross-references

Emerged Reefs  
 Huon Peninsula, P.N.G.  
 Indonesian Reefs  
 Microatoll  
 Radiocarbon (<sup>14</sup>C): Dating and Corals  
 Sclerochronology  
 Sea-level Indicators  
 Submerged Reefs  
 Uranium Series Dating

## EAST INDIES TRIANGLE OF BIODIVERSITY

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## Synonyms

Centre of diversity; Coral triangle; Indo-Australian Arc; Indo-Malayan centre of maximum diversity; Oost-Indischen Archipel (Dutch); The Malay Archipelago



## Definition

The East Indies Triangle of biodiversity (EITB) refers to the region between the Indian and Pacific Oceans, including Indonesia, the Philippines, Papua New Guinea, Solomon Islands, Timor Leste, part of Malaysia, and some adjacent land and sea. The boundaries of the region have been variously drawn over time, based on estimations of where the greatest marine biodiversity is found (Figures 1 and 3).

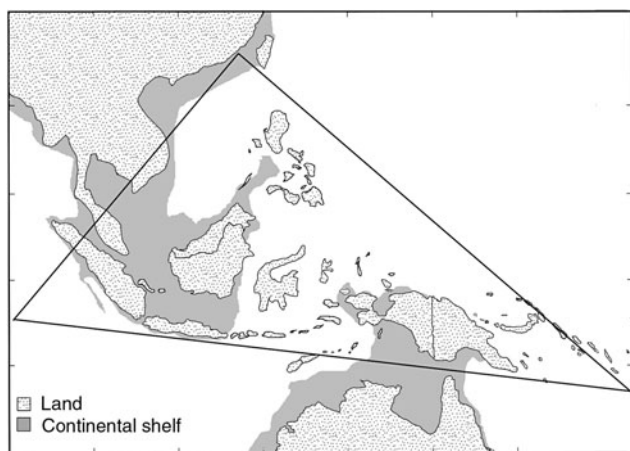
## Introduction

Many animal and plant groups show their greatest species richness in the EITB, resulting in a general biodiversity not matched elsewhere in the world. This richness is evident in coral reefs and associated habitats as well as the deep seas that surround them (Paulay, 1997; Allen, 2002; Hoeksema, 2007; Cairns, 2007; Renema et al., 2008). Although species are still being discovered, and precise numbers not available for any group, it is now clear that the greatest number of reef-building coral genera and species occur in this region (Hoeksema, 2007 and contained references), as well as reef-associated fish, mollusks and crustaceans (e.g., Findley and Finley, 2001; Allen, 2002; Meyer, 2003; Table 2 of Hoeksema, 2007). Less documented in compilations but evidenced in numerous taxonomic and other sources is a great richness of small commensal, cryptic, parasitic, and symbiotic organisms from these and other groups such as Echinodermata, associated with coral reef organisms. There is strong scientific interest in identifying the source of this high biodiversity.

Although mainly interested in terrestrial organisms, the great evolutionary biologist and biogeographer Alfred Russell Wallace was aware of the significance of the marine fauna of the Malay Archipelago, commenting after a drift in a boat across Ambon Harbor that “There is perhaps no spot in the world richer in marine productions,

corals, shells and fishes, than the harbor of Amboyna” (Wallace, 1869). A triangle (Figure 1) was used to enclose the general area of the marine East Indies by Briggs (1987), who later provided persuasive evidence to demonstrate that this was also a “center of origin,” from which marine animals dispersed in all directions (Briggs, 1992). Another strong influence on the “center of origin” hypothesis came from a study of the distribution of coral genera throughout the Indo-Pacific (Stehli and Wells, 1971). This idea had much acceptance and has strongly influenced thinking about the marine biogeography of the Indo-Pacific: however, it begged the question of how so much origination occurred, and it was not formally testable. The biogeography of land animals and plants within the same region has been extensively tested against a growing body of knowledge about the tectonic history of the Southeast (SE) Asian region, and timing of events relevant to large-scale isolation and subsequent evolution of fauna and flora (Audley-Charles, 1987; Whitmore, 1981, 1987; Michaux, 1991; Metcalf, 2001). These findings indicate that the complexity of geological and hydrodynamic events and variety of their timing have contributed to a layering of evolutionary and biogeographic patterns in this region.

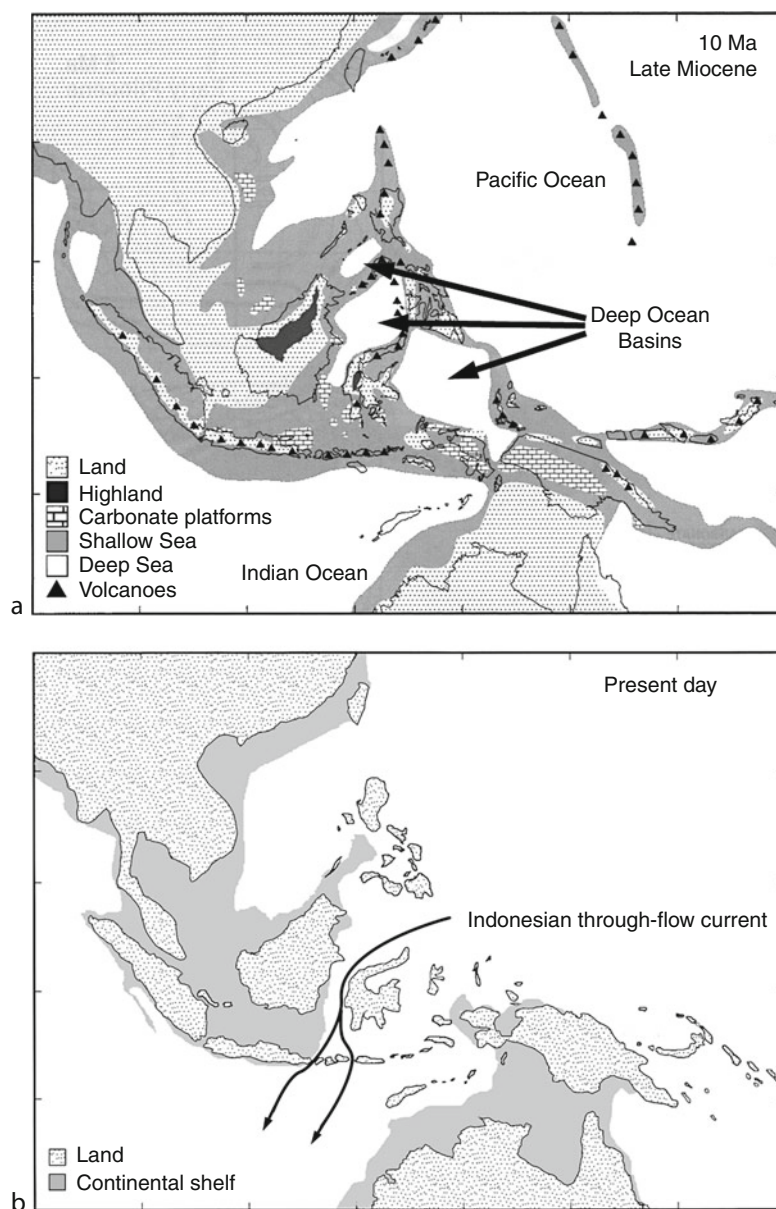
This kind of information has been more difficult to assess for the marine biota. The sea, which isolates land masses, connects marine habitats. It carries the larvae and/or adults of marine animals, while land masses form the main isolating barriers to sea regions (Pandolfi, 1992). Eustatic events (sea-level changes) cause marine connections to close and reopen from low to high sea stands. Progress in assessing the evolutionary and biogeographic consequences of this history of changing land and sea distribution, sea levels, and connectivity has been made using a number of approaches (e.g., Pandolfi, 1992; Barber et al., 2000; Bellwood and Wainright, 2002; Kirkendale and Meyer, 2002; Wallace, 2001, 2002; Wallace et al., 2002; Hoeksema, 2007, and contained references).



**East Indies Triangle of Biodiversity, Figure 1** The area of the central Indo-Pacific designated as the “East Indies centre of evolutionary radiation” by Biggs (1987).

## Tectonic and oceanographic basis

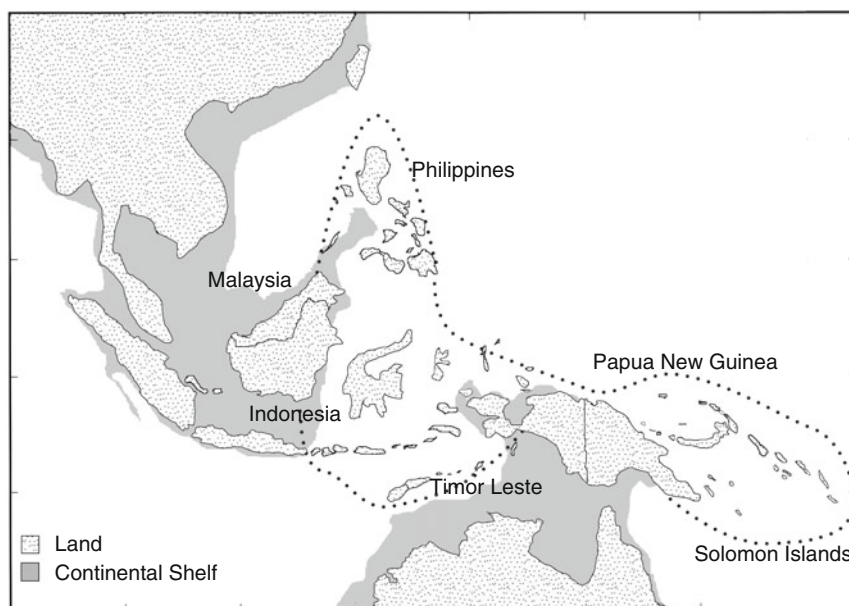
Coral reefs, and indeed even locations suitable for the development of reefs, were lacking in the central Indo-Pacific during the Paleogene period (65–23 million years ago), whereas extensive development of coral reefs was taking place in a warm, shallow Mediterranean region (Wilson and Rosen, 1998; Perrin, 2002). At this time, a 3,000-km-wide oceanic void, with few shallow water areas or landmasses, existed between Australia and the Southeast Asian mainland (Wilson and Rosen, 1998). This gap gradually narrowed as the Australasian craton moved northward, and shallow water areas emerged, which were eminently suitable for the development of coral reefs (Wallace and Rosen, 2006). The carbonate record in SE Asia indicates that marine and atmospheric conditions for enhanced coral growth and therefore reef formation gradually improved during this process, leading to an “order of magnitude expansion of shallow carbonate



**East Indies Triangle of Biodiversity, Figure 2** Influences proposed to have contributed to the world-greatest biodiversity and distribution of staghorn corals (genus *Acropora*) in the Indo-Australian arc by Wallace (2001, 2002). (a) Separation of the Pacific and Indian oceans, at its most effective during the Late Miocene: deep ocean basins also developed around this time and are proposed to have influenced the evolution of endemic species (Based on Miocene land and sea forms from Hall, 1998). (b) Invasion of the eastern Indian Ocean by Pacific species is now promoted through the influence of the Indonesian through-flow current.

areas” in the Early Miocene (Wilson, 2008). The collision of the Asian and Australian plates produced today’s island archipelagos of SE Asia – the EITB – a composite of fragments which came from various locations throughout the now Indo-Pacific (Michaux, 1991; Hall and Blundell, 1996; Hall and Holloway, 1998). Volcanism and localized dynamic change due to earthquakes and tsunamis still impact on coral reefs in the region (see Wilkinson et al., 2006 and entry *Tsunami*).

The EITB archipelago consists of two broad types of islands and reefs. Some sit on the continental shelf of the Asian and Australian continental plates, and their surrounding seas are shallow (<200 m). Others rise from the deep waters between the shelves (depths to 3,000 m). The greatest diversity of corals and fishes is in the latter non-continental area (“Wallacea”), where the deep seas have allowed reefs to persist continuously for thousands to millions of years, through sea-level changes in excess



**East Indies Triangle of Biodiversity, Figure 3** Boundaries of the region covered by the Coral Triangle Initiative (*dotted line*), encompassing six countries as indicated.

of 100 m that periodically left the shelf reefs and their own shallow portions high and dry. Another key feature of the region is its oceanography (see entry *Indonesian Reefs*). The most significant feature of which is the Indonesian through-flow, a seasonably varying flow of water which travels southwestward from the Pacific Ocean through central Indonesia into the Indian Ocean (Gordon and Fine, 1996; Shriver and Hurlburt, 1997). A third feature of the area is the great variety of habitat types it affords for populations of coral reef species and reef development, from shallow sheltered bays to deep swell-exposed outer slopes (see entry *Corals: Environmental Controls on Growth*). This range of environments and habitats is a critical contemporary determinant of the EITB's diversity, distribution, and abundance of reef species, as outlined, for example, in a distribution study of mushroom corals (family Fungiidae) by Hoeksema (2007).

The EITB's richness of coral species (Veron, 1995; Paulay, 1997; Hoeksema, 2007) is also exemplified by staghorn *Acropora* corals, whose greatest diversity of species per area occurs there (Wallace and Wolstenholme, 1998; Wallace et al., 2001). These authors postulate three major evolutionary and biogeographic influences on the current species richness and distribution patterns of *Acropora*, which are also likely applicable to the majority of coral reef genera (Figure 2). Present *Acropora* species patterns appear to reflect speciation in the Indian and Pacific Oceans due to genetic isolation of subpopulations caused by Mid Miocene tectonic events, leading to a barrier between the oceans (Figure 2a). At the same time, deep ocean basins were formed (Hall, 1998), which are proposed to have influenced the origination and retention

of endemic species (Figure 2a). Last, in more recent time, the Indonesian through-flow current (Gordon and Fine, 1996) would have allowed larval dispersal of Pacific species into the Indo-Australian Arc and through to the eastern edge of the Indian Ocean, while central and western Indian Ocean species remain isolated because of the absence of a return flow (Figure 2b).

### Coral triangle conservation initiative

Concerns have been raised for the future of the EITB, based on the recognition of the general effects on coral reefs of decades of destructive fishing, overfishing, and pollution (Wilkinson, 1998), compounded by severe bleaching events in the Indian and Pacific oceans (1998 and 2002) and the 2004 Asian tsunami (Wilkinson et al., 2006) and other major changes in sea-surface temperature and ocean chemistry due to global climate change (Lough, 2000; Kleypas et al., 2001). To indicate more accurately the extent of the highest biodiversity region, the boundaries of the "triangle" were changed (Figure 3). In 2009 an inter-governmental policy agreement, the "Coral Triangle Initiative" (CTI), was signed by the governments of Indonesia, Malaysia, Papua New Guinea, the Philippines, the Solomon Islands, and Timor-Leste, all countries with territory in the new "triangle" (Anonymous, 2009).

The goals of CTI are: (1) as a priority, to designate and effectively manage "priority seascapes" encompassing the major high-diversity coastal regions; (2) to establish an ecosystem approach to fisheries management; (3) to establish and effectively manage a system of marine protected areas; (4) to establish a regionwide early action plan for



climate change adaptation and (5) to improve the conservation status of sharks, sea turtles, seabirds, marine mammals, corals, seagrass, mangroves, and other identified threatened species (Anonymous, 2009). Government sponsorship of the CTI is supplemented by commitments from major non-government organizations such as WWF, the Nature Conservancy and Conservation International, as well as governments of neighboring and other countries.

## Summary

Biodiversity and endemism of the world's living coral reefs are greatest within the waters and islands between the Asian and Australian continental shelves. The origins of this situation relate to the complex tectonic history of the region, and the hydrological systems associated with it, both now and in the past, as well as to the great extent and variety of coral reef habitats present. This knowledge, along with insights from molecular genetics and improved data about the biodiversity, paleontology, and phylogeography of many animal and plant groups, is contributing to a better documentation of marine faunal and floral patterns of the region. However, much remains to be understood, and many new species await description. An initiative to provide broad conservation management for coral reefs within the territories of six countries aims to provide protection for all species in the region by a series of measures.

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## Cross-references

[Conservation and Marine Protection Areas](#)  
[Eastern Indian Ocean – Northern Sector](#)  
[General Evolution of Carbonate Reefs](#)  
[Global Ocean Circulation and Coral Reefs](#)  
[Indonesian Reefs](#)  
[Reef Interconnectivity/Larval Dispersal](#)  
[Tsunami](#)  
[Volcanic Disturbances and Coral Reefs](#)

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## EASTERN CARIBBEAN CORAL REEFS

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## Synonyms

Holocene reefs of the SE Caribbean; Modern SE Caribbean reefs; SE Caribbean reefs

## Definition

Eastern Caribbean Coral Reefs are biologically mediated structures that have formed since the last lowstand of sea level and are associated with islands and platforms to the east and south of the Island of Hispaniola in the Caribbean Sea.

## Reef types

The present-day Caribbean Sea was formed between 200 and 130 million years ago as the Caribbean Plate moved eastward, forcing North and South America apart (Pindell et al., 1988). The eastern Caribbean is defined on the north by faults and islands, on the south by South America, and to the east by the Antilles Arc and the Atlantic Ocean (Figure 1). With a few notable exceptions, most islands in the Antilles chain have igneous origins and steep slopes that leave little opportunity for extensive barrier reef formation.

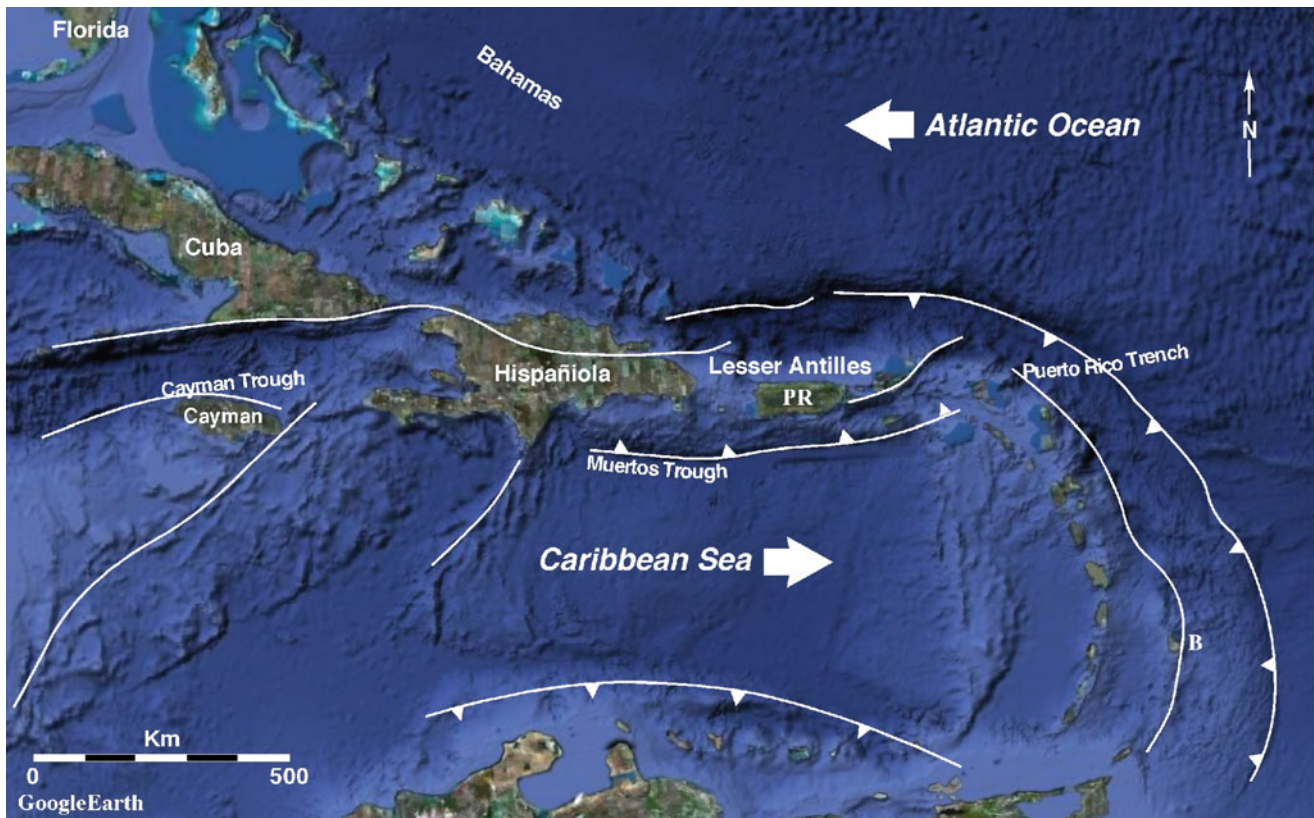
For the purpose of this chapter, Caribbean reefs are divided into three categories: fringing, barrier, and shelf-edge reefs. This provides a simple frame of reference for the discussion below, and is not proposed as an alternative to any of the classification schemes that already exist.

*Fringing reefs* form along steep insular margins (Figure 2). As a result, reefs are close to shore, and lagoons are small and shallow (<100 m wide and <2 m deep). Individual reefs rarely exceed a few hundred meters in length. Where the foreshore slope is gentle or flat, *barrier reefs* form 0.5–3 km from shore in front of well-developed lagoons (Figure 3). They extend for 1–2 km alongshore and effectively protect the bay from open-Caribbean processes. Their location is often tied to antecedent topographic benches, but they are also formed atop loose rubble shoals dominated by bioclastic debris (Adey and Burke, 1976) that may reflect an earlier phase of reef development in which calcification and bioerosion were in balance. Along the margins of many islands and shallow carbonate banks, *shelf-edge reefs* form still-submerged structures that range from thin veneers that mimic antecedent topography to elevated rims that owe their present shape to significant Holocene accretion (Figure 4a). These features can sit seaward of shallower reefs (e.g., Puerto Rico, Hubbard et al., 1997) or stand alone, especially along the edges of submerged platforms (e.g., Saba Bank, Macintyre, 1972). Regularly spaced sand channels that are oriented downslope serve as short-term repositories for excess sediment and as conduits for the offshore transport of sand, especially during storms (Hubbard, 1992). Where they front steep islands (e.g., Cane Bay on St. Croix), the greatest coral abundance often occurs near the shelf edge where the adverse effects of terrestrial runoff are reduced (Figure 4b; Hubbard et al., 1990).

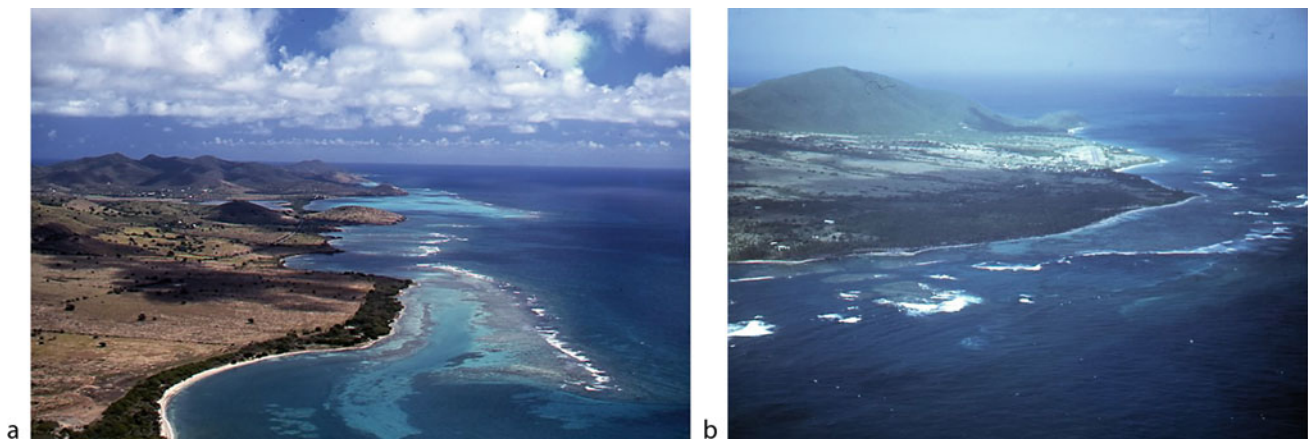
## Oceanography and reef-community structure

Caribbean reef-crest communities tend to vary from massive algal ridges in the eastern Windward Islands, to *Acropora*-dominated reef crests in the Leeward Islands to mostly hardgrounds with scattered, massive corals and fewer branching species to the far west (Adey and Burke, 1977; Geister, 1977). Adey and Burke (1977) demonstrated that wave energy and water quality were important controls over what the reef-crest community looks like and at what depths zonation boundaries occur. As





**Eastern Caribbean Coral Reefs, Figure 1** Location map showing the major physiographic features in the eastern Caribbean. The Caribbean plate is bordered on the north by a series of left-lateral faults and the Greater/Lesser Antilles. The southern boundary sits near South America. Most of the Windward and Leeward Islands are part of an island arc formed as the westward-moving Atlantic Plate slipped beneath the eastward-moving Caribbean. "PR" and "B" mark Puerto Rico and Barbados, respectively. Faults after Pindell et al. (1988).



**Eastern Caribbean Coral Reefs, Figure 2** Air photographs of fringing reefs along the south coast of St. Croix (a) and the eastern side of Nevis (b). In both areas, the nearshore slope drops quickly to the insular shelf and forces the reefs against the coast. Photos by permission of the author.

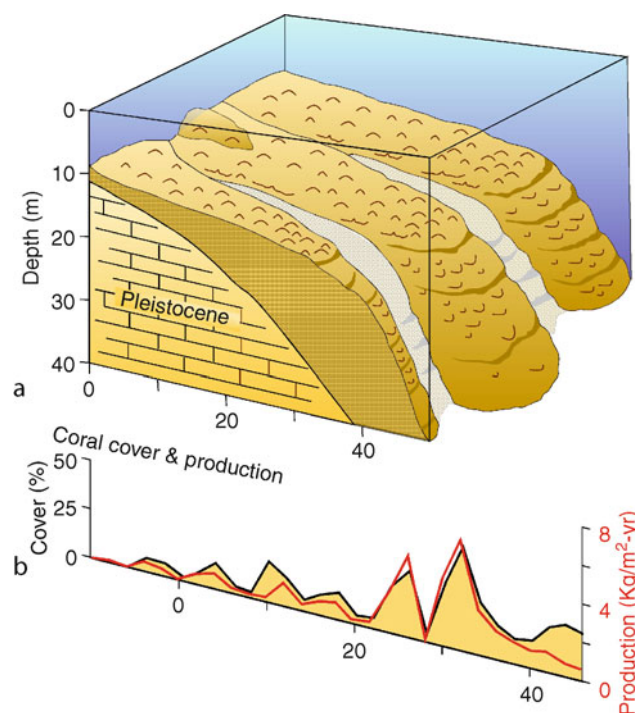




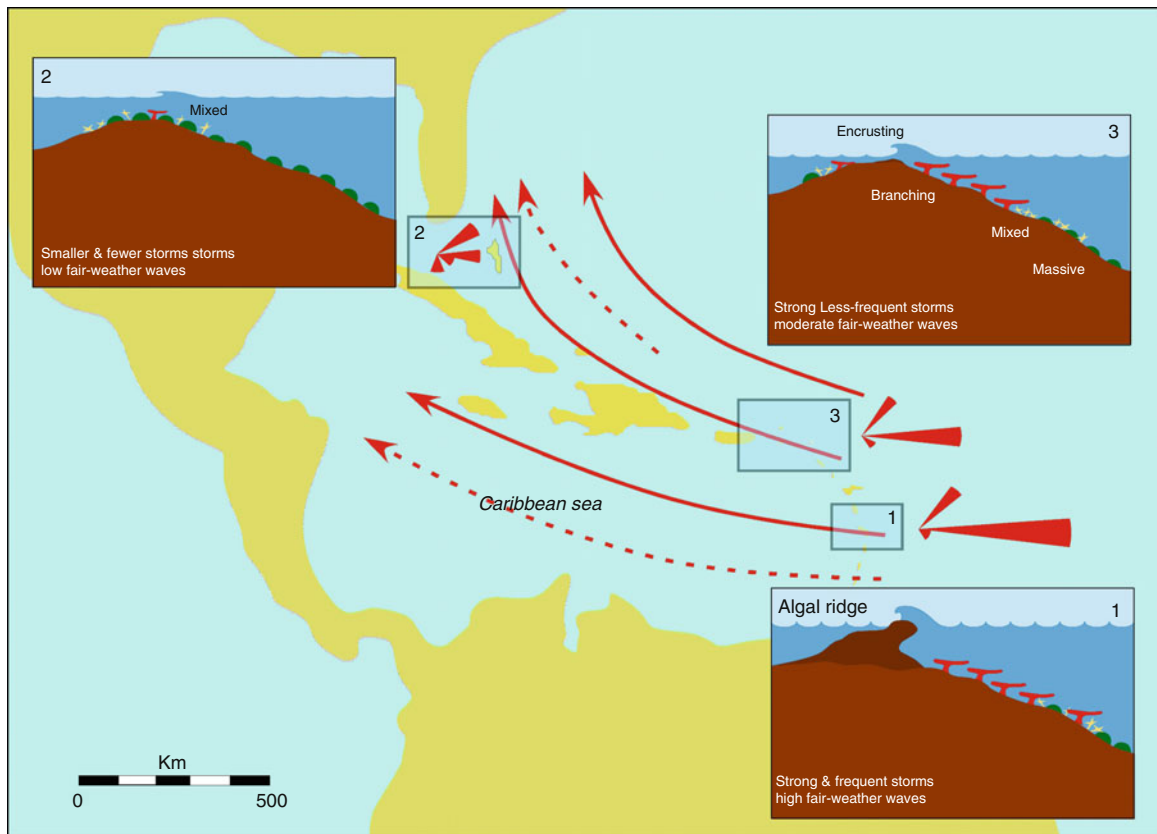
**Eastern Caribbean Coral Reefs, Figure 3** Air photograph of the barrier reef fronting Christiansted Harbor on the north side of St. Croix. The lagoon is ca. 1 km across. These reefs are significantly further offshore than fringing reefs and provide a clear line of demarcation between offshore and lagoonal processes. Photo by permission of the author.

a proxy, they proposed a “wind index” to reflect the gradual loss in wind and wave energy moving northward toward the “horse latitudes.” This is clearly reflected in the rose diagrams in Figure 5 based on synoptic, fair-weather wave data compiled by the US Navy. Hubbard (1989) proposed that hurricane frequency and intensity might also play a role in this equation. Using detailed records for the previous century, the likelihood of major storms passing through 1-degree grid squares across the Caribbean and western Atlantic were tabulated. Contours of the highest return frequencies were used to identify the most likely storm tracks through the region (red arrows in Figure 5).

The highest fair-weather waves plus the most common and severe storms occur near the boundary between the Windward and Leeward Islands. Near Guadalupe, Category 3–5 hurricanes strike almost annually, minimizing branching acroporids along the reef crest. In the interim, Atlantic swell creates a high-energy environment that discourages grazing. The result is an accumulation of coralline algae that build thick, wave-resistant structures (Adey and Burke, 1976, 1977: see area 1 in Figure 5). In the northwestern Caribbean and western Atlantic (area 2 in Figure 5), storms are still common but generally less severe. Fair-weather wave climate is benign compared to the more exposed Windward Islands. Because *Acropora palmata* is extremely sensitive to sediment stress (Adey et al., 1977b; Rogers, 1983), it relies on wave action to clear sediment. Thus, a reef-crest community dominated by branching corals is difficult to support in all but the most energetic areas (e.g., where winter swell impacts the Bahamas). Smaller waves also make grazing easier, precluding the accumulation of thick coralline crusts (Adey and Burke, 1977). Reef crests dominated by hardgrounds and massive corals tend to be



**Eastern Caribbean Coral Reefs, Figure 4** (a) Stylized drawing of a Caribbean shelf-edge reef. In this example, the antecedent Pleistocene topography has been accentuated by Holocene accretion. Channels through the reef facilitate sediment storage and removal. (b) Graph summarizing the abundance of corals (black line) and carbonate production (red) across the narrow insular shelf at Cane Bay on St. Croix. Note that the greatest coral cover and carbonate production occur near the shelf edge where sedimentation is low. After Hubbard et al. (2008) with permission by Springer.



**Eastern Caribbean Coral Reefs, Figure 5** Caribbean reef type versus fair-weather wave climate and storm frequency. The “petals” on the “rose diagrams” (in red) are proportional to the total wave energy from a particular direction, based on wind and wave data from the US Navy Synoptic Survey of Meteorological Observations (SSMO). The solid (hurricanes) and dashed (tropical storms) arrows characterize the primary storm paths through the region. Major storms cross directly through the easternmost Caribbean (area 1) on an annual basis. High storm frequency and vigorous day-to-day waves discourage acroporids and intense grazing. The result is an accumulation of thick and wave-resistant ridges built by coralline algae (Adey and Burke, 1977). *Acropora palmata* is often found but in deeper water where wave action is buffered. The more modest wave climate and the greater proximity to sources of terrestrial sedimentation in the northwestern Caribbean (area 2) favor massive corals over branching *A. palmata*, which depends on wave action to clear sediment. In the northern Leeward Islands and the Lesser Antilles (area 3), intermediate fair-weather wave climate and moderate storm intensity/frequency provide an ideal environment for branching and smaller encrusting forms in shallow water. From Hubbard et al. (2008) with permission of Springer.

the norm. The intermediate wave climate of the northeastern Caribbean (area 3 in Figure 5) provides the ideal environment for a well-zoned reef front that ranges from encrusting and branching forms near the surface to massive and platy corals at greater depths. Because these islands exist in a transitional area, relatively small changes in shoreline orientation can result in any of the three reef-crest communities just described, depending on exposure and storm proximity. For example, well-developed *A. palmata* reefs flourished along the northeastern coast of St. Croix until the arrival of White Band Disease in the late 1970s. In contrast, the south side of the island is more exposed to southeasterly Caribbean swell and storms passing to the south (Figure 5). This encourages algal ridges that are similar to but less extensive than those found in the northern Windward Islands (Adey, 1975). Along the less exposed northwestern shelf, massive corals dominate

the sloping shoreface, and *A. palmata* has been a minor contributor to reef accretion over at least the past 3,500 years (Hubbard et al., 1986).

### Holocene reef geology in the southeastern Caribbean

Throughout the late 1970s, the Smithsonian Institution mounted an aggressive investigation of late Holocene reefs throughout the Caribbean. The articles from these studies still provide the most comprehensive treatment of shallow reefs in the region (Adey, 1975; Adey et al., 1977a,b; Adey and Burke, 1976, 1977). Since these early studies, core investigations have expanded to include other shallow reefs on St. Croix (Hubbard et al., 1986, 2005; Burke et al., 1989), Antigua (Macintyre et al., 1985), and Vieques (Macintyre et al., 1983) plus deeper shelf-edge features

(Adey et al., 1977b; Hubbard et al., 1986, 1997, 2005, 2008; Macintyre et al., 1981) and abandoned Holocene reefs that formed during the most rapid part of the Holocene sea-level rise (Fairbanks, 1989; Bard et al., 1990).

### Deep Holocene reefs

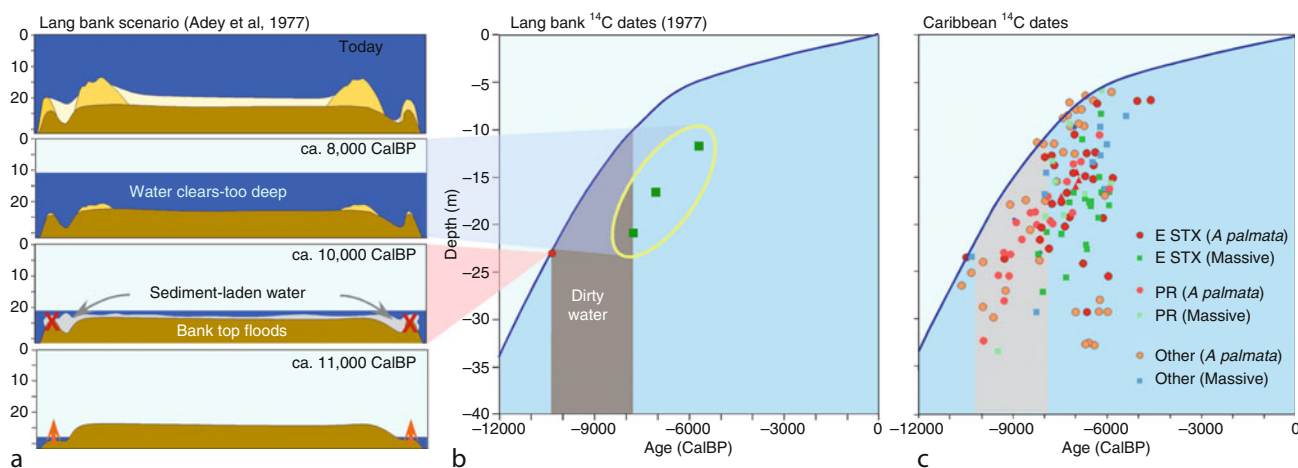
Along the steep slopes beneath many Caribbean shelf margins, submerged ridges and terraces were flooded by rapidly rising sea level (Jukes-Browne and Harrison, 1891; Vaughn, 1916; Davis, 1926; Macintyre, 1972). Cores by Fairbanks (1989) have documented an early Holocene origin for three submerged reefs off Barbados (Figure 6b: RFG-7, 9, 12), and similar scenarios are probable throughout the region (e.g., see Sherman et al., 2010 for a discussion of deep mesophotic reefs off southwestern Puerto Rico). The ephemeral nature and sudden back-stepping of the deep reefs off Barbados were explained as responses to two decameter-scale jumps in sea level starting ca. 14,000 and 11,400 years ago. This was supported by isotopic data that suggested a rapid release of meltwater at these times (Fairbanks, 1989). Stanford et al. (2006) have proposed that the older 16 m rise in sea level could have occurred in as little as 200 years. Most recently, Bard et al. (2010) have called the second jump into question based on new core data from Tahiti.

Regardless of their absolute history, these cores demonstrate that well-developed Holocene reefs built structures

10–20 m thick along the steep margin of Barbados under a regime of rapidly rising sea level (avg.  $\sim 5\text{--}7$  m/ky). Each reef was eventually abandoned and a new one formed upslope (back-stepping). It should be noted that the top of each abandoned reef and the base of its upslope neighbor coexisted at similar depths (see Fig. 1 in Fairbanks, 1989). Furthermore, *A. palmata* remained dominant near the top of each abandoned reef as a similar community was developing along the new, upslope feature. It has been suggested that Pleistocene lowstands have necessitated a period of highstand “reassembly” in which the zonation pattern was reestablished (Jackson, 1992; Pandolfi, 1996). Inherent in this concept is a significant disruption of community structure associated with low-stands of sea level. However, the potential for community disruption even during the fastest sea-level change is small on the temporal scale in which larval dispersal and recruitment occur. The Barbados cores demonstrate a clear connection between successive reefs that allowed community structure to be transmitted upslope even when individual reefs could not.

### Shelf-edge reefs

The next major episode of reef building began with platform flooding throughout the region. Three cores along the southern margin of Lang Bank, east of St. Croix, provided our first glimpse of these features and became the



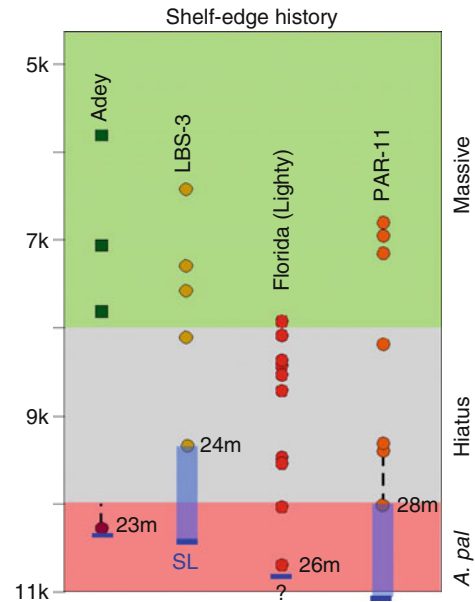
**Eastern Caribbean Coral Reefs, Figure 6** (a) Scenario of reef development on southwest Lang Bank east of St. Croix as described by Adey et al. (1977b). Earliest shelf-edge *Acropora palmata* reefs (red circle in (b)) were killed ca. 10,000 years ago by sediment-laden water shed from Lang Bank during flooding, a condition that persisted until 8,000–7,000 years ago (“Dirty Water” in (b)). By the time these “inimical bank waters” cleared, water depth was too deep for fast-growing *A. palmata*, and the new reefs were dominated by massive species (green squares in (b)), which led to slower but continuous accretion until today. (b) Calibrated radiocarbon ages from Adey et al. (1977b). Because of similar platforms elsewhere in the region, it was presumed that this pattern would generally persist for similar sites as new core data became available. (c) Summary of available radiocarbon data for Caribbean shelf-edge reefs. Other reefs on Lang Bank (E STX: Hubbard et al., 2005), Puerto Rico (PR: Hubbard et al., 1997; Hubbard, unpublished data), and elsewhere in the western Caribbean/Atlantic (Other: Lighty et al., 1982; Macintyre et al., 1985; Toscano, 1996; Toscano and Lundberg, 1998) flourished throughout the period of “dirty” water proposed for Lang Bank and extrapolated to other Caribbean sites in existing models (shaded gray). These reefs were dominated by branching *A. palmata* closest to the shelf edge and massive species in the backreef at sites where multiple cores were taken. After “Coral Reefs: Biology, Geology & Politics: an e text” with the author’s permission.



foundation of a broader Caribbean model for Holocene reef development. According to Adey et al. (1977b), early *A. palmata* reefs formed near the shelf break by at least 10,500 cal BP, but were soon killed by turbid water derived from the reworking of long-exposed terrestrial silts and clays atop the platform and landward of their core site (Figure 6a; “inimical bank waters” of Schlager, 1981). Nutrients adsorbed to fine-grained sediments (especially siliciclastic clays) could also have discouraged calcification (phosphorous) and encouraged algae (nitrogen), as well as bioerosion, which is also favored by increased nutrients (Moore and Shedd, 1977; Edinger and Risk, 1997). Based on the Lang Bank cores, Adey (1978) concluded that, “from about [10,200] to [5,800] years ago, apparently very little reef development occurred on the island of St. Croix.” (Bracketed values are corrected from the raw  $^{14}\text{C}$  measurements.) Reef accretion may have started again on Lang Bank as early as 7,800–7,000 years ago (adjusted from the raw  $^{14}\text{C}$  ages in their Fig. 4 of Adey et al., 1977b).

More recent shelf-edge cores from St. Croix (Hubbard et al., 2004, 2005, 2008) confirm that the inhibition of reef development around the island was not as dramatic as has been assumed. This pattern is repeated in cores from similar systems off southwestern Puerto Rico (Hubbard et al., 1997) and Florida (Lighty et al., 1978; Toscano and Lundberg, 1998), where “inimical bank waters” played a role that was more variable and of shorter duration than previously described (Figures 6c and 7). Cores from the northern margin of Lang Bank show a delay in reef accretion until ca. 8,000 years ago (Hubbard et al., 2005, 2008, unpublished data). However, these reefs were dominated by *A. palmata* and not massive species as had been assumed. Along the southern margin, less than 5 km east of the Smithsonian core site, accretion had started by at least 9,300 years ago. Based on the corrected curve of Lighty et al. (1982) (see Hubbard et al., 2000, 2002, 2005; Toscano and Macintyre, 2003 for details), the antecedent Pleistocene surface would have flooded less than 1,000 years prior (Figure 7). As was the case to the north, branching corals dominated the reef crest and continued to do so until after 6,500 cal BP (Hubbard et al., 2004; Hubbard, 2009b). Along the eastern tip of Lang Bank, the oldest date from a core through the reef crest was 8,000 cal BP, but nearly 5 m of undated section separates it from the underlying Pleistocene surface at a depth of over 30 m below present sea level. Based on the accretion rate for the upper 12 m of core, this reef could have started as early as 9,500 years ago, with a longer lag period (~2,000 years), despite its position on the most upwind margin Lang Bank. Thus, *A. palmata* reefs were present along the upper shelf rim as early as 9,500 years ago, and, once accretion began at any site, reef building and community structure remained constant for at least 1,000 years beyond the proposed IBW-hiatus (Figures 6c and 7; Hubbard et al., 2008).

Along the southwestern corner of Puerto Rico, samples 1–2 m above the base of the Holocene section at two shelf-



**Eastern Caribbean Coral Reefs, Figure 7** More detailed summary of selected Caribbean shelf-edge cores. The colored bands correspond to the intervals of reef start-up (red), abandonment due to “inimical bank waters” (gray) and recolonization by slower-growing massive corals (green) proposed by existing Caribbean models. Circles denote *Acropora palmata*; squares are massive species. Dark blue bars show depths of antecedent substrates below present sea level. Light blue shaded intervals indicate nonaccretion following bank flooding at each site. Reef accretion between 10,000 and 8,000 years ago was clearly more important than has been assumed. Also, accretion by rapidly growing acroporids continued afterward at many sites.

edge sites yielded radiocarbon ages of 9,300 and 9,500 cal BP (Hubbard et al., 1997), consistent with the oldest ages from the shallow rim of Lang Bank sitting at similar depths. As on St. Croix, both sites were dominated by *A. palmata* from the time when they first started to build until ca. 7,000 years ago (i.e., they flourished across the proposed hiatus and beyond). Based on the average accretion rate for the two cores (4.3 m/ky) and the documented antecedent depth of –27 m, little or no lag existed between shelf flooding and the initiation of reef preservation (Figure 7).

Figure 6c summarizes available data for ages and depths of shelf-edge reef samples throughout the Caribbean. Figure 7 provides more detail for individual shelf-edge cores from Lang Bank, Puerto Rico, and Florida. The density of data is lower prior to 8,000 years ago, owing to fewer cores having been recovered from these more logistically difficult environments. Nevertheless, it is clear that reef accretion did occur within much of the interval between 10,000 and 6,900 cal BP on both St. Croix and elsewhere in the Caribbean (compare Figure 6b and c). Furthermore, once *A. palmata* reefs were established at a particular site, their community structure remained constant until some time after 7,000 cal BP.

### Inner-shelf reefs

As the inner shelves continued to flood and sea level slowed further, the locus of reef development shifted to progressively shallower sites. As was the case for the deep reefs off Barbados, this “back-stepping” often began before the shelf-edge reefs were abandoned. On Lang Bank, reef accretion along the margin continued until ca. 6,500–6,000 cal BP, over a thousand years after now-emergent reefs to the west had already started up closer to the shore (Adey, 1975; Burke et al., 1989; Hubbard et al., 2005; Macintyre et al., 2008). Similarly, when the shelf-edge reefs off southwestern Puerto Rico were abandoned (~6,800 cal BP), the mid-shelf reefs had already been active for nearly a millennium (Hubbard et al., 1997). In many instances, these shallower reefs sat atop antecedent highs, but Adey (1988) showed that some early reefs stabilized mobile bioclastic sand shoals – perhaps equivalent to the detrital intervals described above for many shelf-edge reefs. It is probably not coincidence that presently emergent reefs started to build to sea level at the same time when barrier islands were forming all around the world. While the sources of material were different, slowing of sea level facilitated the filling of accommodation space in both instances.

### What have we learned?

While this section focuses on the southeastern Caribbean, lessons have been learned that are applicable to the broader Caribbean. Cores off Barbados (Fairbanks, 1989) have verified earlier suggestions that reefs below the edges of many platforms are probably relict Holocene features left behind by rapidly rising sea level (Vaughan, 1916; Macintyre, 1972). The potential importance of sudden and rapid upward shifts in sea level has also been clearly demonstrated.

### The role of “inimical bank waters”

The earlier models of Adey (1978) and Macintyre (1988) introduced the idea that turbid water associated with platform flooding retarded reef building for up to 4,000 years along Lang Bank until water quality improved. While poor water quality undoubtedly played an important role in early shelf-edge reef accretion on St. Croix, its effects were more complex and perhaps shorter-lived than has been assumed. Throughout the region, active *A. palmata* reefs built uninterrupted across much of the interval for which reef-building was previously characterized as minimal. Many of these reefs continued to flourish until 7,000 cal BP and beyond.

Bioclastic debris near the base of many cores may reflect an additional mechanism that is more indirectly related to flooding – intense bioerosion driven by elevated nutrient levels (Schlager, 1981; Hallock and Schlager, 1986). Adey and Burke (1976) described significant detrital intervals beneath the shallow “bank-barrier” reefs on northeastern St. Croix and concluded that this represented stabilization by an early coral community followed by active coral-dominated accretion. Similar patterns have

been documented along the shelf margins described above and may represent an early standoff between carbonate production and bioerosion. An important lesson here is that the oldest preserved corals need not reflect the first appearance of coral communities with reef-building potential. Thus, water quality may have been adequate to support widespread coral growth but not reef accretion.

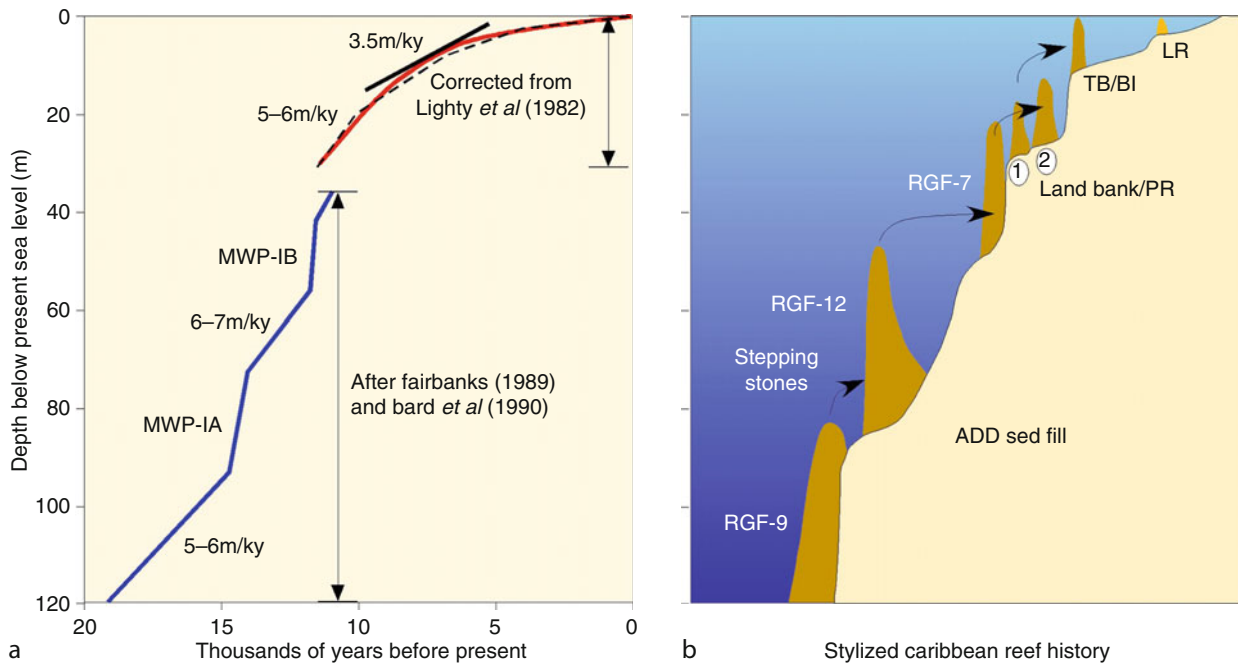
### St. Croix as a “Caribbean model”

Because many shelf and platform margins throughout the Caribbean sit at water depths similar to Lang Bank, the scenario from St. Croix was extended to western Atlantic platforms under the influence of medium to high energy: “Where the shelf edge is between 10 and 30 m, early Holocene reefs were killed off owing to turbidity, and continuous Holocene reef building did not occur adjacent to deep oceanic waters” (Adey, 1988). “By the time water conditions returned to normal, the advancing seas were too deep to allow shallow-water communities of *A. palmata* to reestablish. The rapid reef growth of these communities was thus transferred to shallow-water substrates adjacent to coastlines” (Macintyre, 1988). More recent studies have shown that local tectonic and varying oceanographic processes have resulted in significant variability in antecedent topography, both regionally (see Fig. 3 in Adey, 1978) and locally (Burke et al., 1989; Macintyre et al., 2008; Hubbard et al., 2005, 2008; Bard et al., 2010). It, therefore, seems more realistic to expect nonsynchronous patterns of shelf flooding, wide variations in the importance of “inimical bank waters,” and varying accretionary histories controlled by the details of antecedent topography and local oceanographic conditions (Hubbard et al., 2008; Macintyre et al., 2008).

### The role of sea level

Figure 8 summarizes our present understanding of Caribbean sea-level rise (a) and reef development (b). The lower sea-level curve is based on core data from Fairbanks (1989) while the upper curve is modified from Lighty et al. (1982). While some studies have challenged the details of this curve (e.g., Gischler and Hudson, 2004), all agree that sea level rose rapidly (avg. ~5–7 m/ky, with shorter-lived episodes of faster rise) until ca. 8,000–6,000 years ago, after which it decreased to rates below 2–3 m/ky.

Whether reefs remain submerged or are close to sea level today was determined primarily by the rate of sea-level rise at the time when they started to build. Hubbard (2009a) calculated an average accretion rate for Caribbean reefs between 3 and 4 m/ky using data from all published Caribbean core logs. The mean accretion rate for reefs dominated by *A. palmata* versus massive species varied by less than 0.5 m/ky at any depth (see their Fig. 6). Similarly, the accretion rate for all paleo-depths between –2.5 and –22.5 m was ~3.5 m/ky, and the differences were statistically insignificant ( $R^2 = 0.003$ ). Short-term accretion rates (i.e., between successive dated samples) were



**Eastern Caribbean Coral Reefs, Figure 8 (a)** Summary of Caribbean sea-level history. The earlier curve (blue) is based on Fairbanks (1989) and Bard et al. (1990). Data for the past 11,000 years (red) are corrected from the Lighty et al. (1982). *Acropora palmata* curve using both proprietary and public-domain software (respectively, Beta Analytic, Inc. and <http://intcal.qub.ac.uk/calib/>). For details, the reader is referred to Hubbard et al. (2000, 2004, 2005) and Toscano and Macintyre (2003). Neumann's (1977) mangrove peat curve for Bermuda (likewise corrected) is shown by the dashed line. (b) Stylized eastern Caribbean profile summarizing available information on reefs between present sea level and a depth of  $-120$  m. The lower profile is drawn from chart data in Bard et al. (2010) and core logs from Fairbanks (1989). The shelf-edge reefs are a composite of St. Croix and Puerto Rico. The inner-shelf reefs are based largely on St. Croix (Hubbard et al., 2008). On St. Croix, the lower shelf-edge reef (1) was active by 10,500 cal BP and reflects the hiatus described in Adey et al. (1977b). The upper shelf-edge reef (2) is based on data from all three sides of Lang Bank. TB/BI = Tague Bay Reef; Buck Island Reef; LR = Long Reef (see Macintyre et al., 2008 for locations). Deeper reefs (RGF-9 m 12, 7) built while sea level was rising rapidly and were sequentially left behind. The shelf-edge reefs (Lang Bank/PR) formed during a transition from rapid to slower sea-level rise. The inner reefs (TB/BI and LR) all formed as sea level was slowing dramatically, and it was easier to fill accommodation space. After "Coral Reefs: Biology, Geology & Politics: an e text" with the author's permission.

variable and did exceed 7 m/ky on occasion. However, these were almost always from short-lived intervals within reefs that were building at much slower rates closer to the regional average of 3–4 m/ky. Similar patterns have been described by Gischler (2007) for Belize and Hopley et al. (2007) for the Great Barrier Reef. Holocene reefs in the western Dominican Republic verify an abrupt change from transgression to regression as the rate of sea-level rise dropped below 3–4 m/ky after 7,000 cal BP (Hubbard et al., 2009).

Early reefs, like those off the southern Barbados shelf, were left behind, despite showing at least brief accretion rates that rivaled sea-level rise. The innermost reefs all around the Caribbean formed around 8,000 years ago as sea level was slowing. This has allowed them to either "keep up" or "catch up" in the interim (Adey and Burke, 1976; Neumann and Macintyre, 1985). The eventual shift in the shelf-edge reef community between 7,000 and 6,000 years ago is enigmatic inasmuch as it occurred at a time when sea level had slowed to the point where it should have been much easier to keep up. This was also

long after bank waters had cleared, and the reefs were still in water depths capable of supporting active accretion. Why *A. palmata* reefs quit throughout the Caribbean, (Hubbard et al., 2005) and why they have shown no evidence of catching up for the past 6,000 years is unclear and may bear on recent events involving this important Caribbean reef building species.

The interaction between sea-level rise and local antecedent topography has been the dominant factor controlling the timing of reef development, subsequent reef accretion patterns, and whether particular reefs are at sea level today. Each episode of reef building followed flooding of slope breaks that provided advantages for reef building (e.g., a hard substrate that facilitated coral recruitment, access to open water for easy sediment removal). Initial coral-dominated accretion lagged behind flooding, owing to a combination of reduced water quality (that retarded coral development) and increased bioerosion (that favored sediment deposition over coral-mediated accretion). Community structure varied from site to site, but *A. palmata* appears to have been the most important



reef crest species along many Caribbean shelf margins until at least 7,000 years ago.

The process of reef drowning and back-stepping often began while the soon-to-be-abandoned seaward reefs were still active. Because depths over the two structures appear to have been similar, it is unclear why the seaward reef would have lagged behind its more protected landward counterpart – which was probably closer to sources of sediment stress. Whatever the sea-level scenario, the movement of larvae from one reef to the next was probably no more difficult than it is today. Thus, efficient larval transfer and a stable reef community can be maintained during periods of rapidly changing sea level even when reef accretion cannot.

### A simpler model

The lower section of the profile in Figure 8b is based on Barbados (Fairbanks, 1989), but similar scenarios probably occurred throughout the region. The shallow reefs are based on St. Croix, but generally mimic Puerto Rico and Florida. Along the shelf-edge, the lower reef (labeled “1”) was cored by Adey et al. (1977b) and formed more than 10,500 years ago. Accretion was compromised as the adjacent ridgetop flooded. Along the raised rim of Lang Bank (labeled “2”), accretion was variable in timing but not structure. At most sites, *A. palmata* dominated the bank top and remained as the primary reef builder until at least 7,000 years ago. Back-stepping to the inner-shelf reefs was variable in both timing (antecedent topography, sea-level elevation and rate of change, physical processes) and community structure (water quality, wave energy). Based on the above discussion, the critical points include:

1. Reef start-up, building, and demise are tied more simply to the relationship between sea-level rise and local topography. In this scenario, less regional synchronicity is anticipated, and whether a reef is presently at sea level is mostly a function of the rate of sea-level rise when accretion began.
2. Both the spatial continuity and temporal persistence of reduced water quality after platform flooding are reduced. Bioerosion was perhaps as important as reduced coral productivity in delaying initial reef preservation.
3. The need for “inimical bank waters” or sudden leaps in sea level to induce reef abandonment or back-stepping (Schlager, 1981) is reduced. Both have undoubtedly played important roles, but the shifting of reefs to shallower sites can be a more orderly and less dramatic process than has been traditionally assumed.
4. Larval dispersal was probably no more difficult during episodes of back-stepping than it is today. Thus, the need for dramatic “reassembly” following deglaciation is minimized.
5. The high accretion rates often cited as “typical” for Caribbean reefs are less common than previously characterized and are rarely representative of the pattern seen throughout the reef in which they were found.

Accretion rates closer to 3–4 m/ky (perhaps 3–6 m/ky on the Great Barrier Reef) are consistent with the decrease in the rate of sea-level rise between 8,000 and 6,000 years ago being a “tipping point” that caused a general shift from transgression to regression.

6. *A. palmata* was probably a more persistent reef builder after platform flooding than has been assumed, and it remained as an important shelf-edge reef builder from 10,000 to at least 7,000 years ago.
7. The eventual decline of *A. palmata* across the region starting around 7,000 years ago is enigmatic inasmuch as any potential for “inimical bank waters” had long passed, sea level was slowing down dramatically, and shelf-edge reefs were well above the accepted depth limit for active reef accretion. Corollary to this, it is not clear why many reefs were abandoned inasmuch as they sat at depths similar to new reefs closer to land and the attendant sources of stress.

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## Cross-references

Barbados  
 Belize Barrier and Atoll Reefs  
 Bermuda  
 Florida Keys  
 Meltwater Pulses  
 Reef Classification, Response to Sea Level Rise  
 West Indian Coral Reef Classification  
 Western Atlantic/Caribbean, Coral Reefs

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## EASTERN INDIAN OCEAN – NORTHERN SECTOR

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### Definition

The northern sector of the eastern Indian Ocean includes the Andaman Sea where fringing reefs are abundant and where many corals appear to show some resistance to elevated temperatures and irradiance levels through the possession of thermotolerant symbiotic algae and enhanced physiological defences.

### Background

The northern sector of the eastern Indian Ocean embraces the Bay of Bengal and also the Andaman Sea, the latter supporting extensive coral reefs which are both high in coral cover and coral diversity (Brown, 2007) and comprising approximately 19% of the surface cover of shallow reefs in the Indian Ocean (Spalding et al., 2001), excluding the reefs of western Australia. Within the Andaman Sea fringing reefs are extensive in the Andaman and Nicobar Islands (India), the Mergui Archipelago (Myanmar), west coasts of Thailand and northwest Sumatra (Indonesia) with limited reef development on the Malaysian coast. Although reefs on the Andaman Sea coast of Thailand have been well worked the majority of reefs in the region have never been visited by scientists because of political restrictions.

The reefs of the Andaman Sea which have been studied in detail have considerable scientific interest, particularly in

the context of changing climatic conditions. Sea temperatures in the region are generally high and change little over the year varying from 28°C in January to a maximum of 29.5°C in May. Over the last 50 years sea temperatures have been rising at a rate of at least 0.126°C per decade (Brown et al., 1996). However, there have been only two extensive bleaching events in 1991 and 1995 which have caused any significant coral mortality – more recent events have been localised with corals frequently recovering relatively quickly after the initial bleaching. The most recent mass bleaching event in the Andaman Sea in May 2010 may however prove a greater test of the resilience of these corals. Almost 20% of the 66 genera recorded in western Thailand host symbiotic algae belonging to Clade D which contains some of the most thermo-tolerant algal types known (LaJeunesse et al., 2010) and intertidal corals, which are abundant throughout the region, boast diverse physiological and biochemical defences to both temperature and light stresses (Brown et al., 2002a; Brown, 2007). The dynamic oceanography of the Andaman Sea and the resulting in-built stress resistance of many of the shallow water corals offer potential for the area to be an important ‘refuge’ during a period of climate change.

### Geological history and sea floor topography

The Andaman Sea has a complex geological history and sea floor topography with major rivers draining into the Bay of Bengal to the north via the Ganges/Brahmaputra delta and also directly into the Andaman basin through the Irrawaddy delta. The latter river makes a significant sedimentary contribution to the Andaman Sea with an annual suspended load of  $300,000 \times 10^3 \text{ mt}$  and an average discharge at its mouth of  $13.6 \times 10^3 \text{ m}^3 \text{ s}^{-1}$ . While sedimentation restricts reef growth in close proximity to these discharges, reefs flourish in inshore turbid settings on all islands and mainland areas bordering the Andaman Sea as well in clearer waters around more offshore islands.

The geological history of the region shapes the topography of the Andaman Sea floor and both the geology and the plate tectonics are extremely complex (Curry, 2005). Here the Indian and Eurasian plates collide and other tectonic features include coupling and decoupling of platelets, crustal movement along fault lines, rotation of continental blocks and the opening of marginal basins, as in the Andaman Sea. There has been much physical upheaval over the last 50 million years in the region with large earthquakes being recorded in the Nicobar islands in 1847, 1881, 1941 and 2004 and 2005 (Bilham et al., 2005). The 2004 earthquake was responsible for the devastating Asian tsunami which caused tragic loss of life across the Indian Ocean together with subsidence of land and reefs in the Nicobars and on the west coast of the Aceh province and uplift of land and reefs on the west coast of Sumatra, and in the Andamans (Meltzner et al., 2006).

The sea floor of the Andaman Sea is dominated by the Malay continental margin with an outer shelf break that occurs with increasing depth southward to a maximum at



7°N latitude with pinnacles of 200 m relief marking the shelf break. The slope descends to a deep terrace, 2435 m deep, before dropping to a trough at 3075 m in the central Andaman Sea. Bounding the western portion of the Andaman Sea is the Andaman-Nicobar Ridge. Major channels cross the ridge and divide the Andaman and Nicobar islands into four groups; the islands are fringed by coral shelves 10–50 km wide west of the islands and 10 km wide on the east. The complex topography of the sea bed around the islands is responsible, at least in part, for the exceptionally dynamic oceanography of the area.

### Oceanography and major physical features

The oceanography of the Andaman Sea is governed by the seasonal reversal of the Asian monsoon. While current flow reverses once a year at shallow depths it is believed that a greater depths of >200 m flow changes three times a year (Potemra et al., 1991). Another critical factor influencing water movement is the semi-diurnal tide with tidal ranges of 1–2 m in the Andaman and Nicobar islands and macrotidal ranges of ~3 m along the Thai coast and >5 m on the Myanmar coastline. The complex topography of the channels described above together with strong tidal influences give rise to some of the largest internal waves ever described (Osborne and Burch, 1980). The waves traverse the Andaman Sea in packets of 4–10 with amplitudes of at least 60 m. Bands of surface rips accompany the waves and these can be observed on satellite images stretching some 10–100 km across the sea surface. The internal waves are a major influence in the transport of energy within the ocean and are likely to have a critical effect on temperature and salinity regimes as does upwelling along the continental shelf (Yesaki and Jantarapagdee, 1981).

Sea levels in the region show both high annual variability and significant anomalies in some years (Dunne and Brown, 2001). Large negative sea level anomalies (>20 cm) are obvious in the long-term record and are a characteristic of the Andaman Sea and eastern Indian Ocean. They are generated as a result of ocean-atmosphere-land interactions that result in a phenomenon known as the Indian Ocean Dipole (Webster et al., 1999). This produces a warming in the western basin of the Indian Ocean with higher sea levels and reduced upwelling while in the eastern Indian Ocean sea levels are depressed and upwelling enhanced. Indian Ocean Dipole events were noted recently in 1997–1998, 2003 and 2006–2007 (Brown, 2007; Behera et al., 2008; Rao et al., 2009). Despite these negative sea level anomalies sea level has been steadily rising on the west coast of Thailand at a rate of 28mm per decade over the last 40 years (Tanzil et al., 2009), a fact confirmed by Church et al. (2004) who showed that sea level was rising faster in the north-eastern Indian Ocean, over the last 50 years, than anywhere else in the world. A possible factor inducing this effect may be the recent trend of declining winter and spring snow cover over Eurasia which causes a land ocean thermal gradient that favours stronger south west monsoon winds across the Indian Ocean (Goes et al., 2005).

### Biology of coral reefs of the Andaman Sea

The geology and oceanography of the Andaman Sea have strongly influenced not only the distribution and morphology of reefs in the region but also their resistance and resilience to environmental perturbations. Extensive intertidal reef flats are found throughout the region with sheltered sites being dominated by *Porites* and faviid species while more wave exposed locations are dominated by branching *Acropora* spp., *Pocillopora damicornis* and *Montipora digitata*. Subtidal reefs on the mainland coast of Thailand are found growing to depths of 5–15 m whereas those on offshore islands are found in depths down to 30 m. The most abundant species in deeper water are *Porites lutea*, *Acropora intermedia*, *A. muricata* and *Porites rus* (Phongsuwan and Chansang, 1992). Similar assemblages are found throughout the Andaman Islands. The reefs of the Andaman Sea are some of the most diverse in the northern Indian Ocean with 353 species reported in recent surveys in Thai waters (Turak et al., 2005). Access to the reefs of the Mergui Archipelago and the Nicobar Islands would no doubt increase this figure markedly.

Other significant facts about the corals of the Andaman Sea include their high algal densities (similar to those recorded around Singapore and in the turbid waters of Jakarta Bay) (Brown, 2007); the abundance of genera hosting Clade D algae (Pettay and LaJeunesse, 2009; LaJeunesse et al., 2010); the exceptionally high skeletal extension of the major frame builder *Porites lutea* (Scoffin et al., 1992); and the acclimatory abilities of both coral host and symbiotic algae when exposed to elevated temperatures, following their exposure to high light levels in the field (Brown et al., 2002a, b). Interestingly, recent work (Tanzil et al., 2009) has shown that over the last 19 years both linear extension rate and calcification of *Porites lutea* at Phuket, Thailand, has declined by 17.7% and 11.3% respectively, possibly as a result of rising sea temperatures which may now be beyond the coral's thermal optimum for calcification.

Despite a generally low level of human disturbance the reefs are subject to natural disturbances which include exposure to high solar radiation and desiccation when sea level is depressed; decreased salinity from heavy rain at low tide, tsunami related damage and reef subsidence and uplift through volcanic activity. Following the Asian tsunami in 2004 174 reef sites were visited within 4 days of the event along the 700km long coastline of Thailand between Myanmar and Malaysia. Results indicated minimal damage to reefs with 105 sites being unaffected or showing very little damage (i.e., 11–30% coral cover affected), while 16 sites displayed moderate damage (31–50% coral cover affected) and 23 were severely damaged (>50% coral cover affected) (Satapoomin et al., 2006). Recovery from tsunami damage in Thailand has been rapid with toppled corals showing re-orientated growth within 2–3 years of the event (Phongsuwan, 2007). Impacts in the Andamans and Nicobars were more severe with over 100 km<sup>2</sup> of shallow intertidal reef flat

being uplifted while in the Nicobars more than 200 km<sup>2</sup> of reef was damaged as a result of subsidence and sedimentation (Wilkinson, 2008). While the loss of shallow water corals was significant it should be recognised that there is a series of uplifted marine terraces evident throughout the coast of South Andaman Island with observations dating back to the mid 1800s (Bilham et al., 2005) confirming an active seismic history in the area. Reports of human damage to reefs are restricted to the Thai coastline and include tin dredging, land reclamation and associated dredging and tourism-related activities (Brown, 2007). Global warming also constitutes a serious threat to all reefs in the Andaman Sea though factors induced by climate change such as rising sea level (Church et al., 2004) and alteration of the timing of the Asian monsoon onset (Kitoh et al., 1997) might act to mitigate bleaching stresses through reduction in light levels and reduction of both temperature and light levels, respectively, at a time of year when these stresses are maximal. Little is known about the aragonite saturation state of waters in the Andaman Sea and so the susceptibility of corals to ocean acidification is, at this stage, unknown.

Interestingly, the shallow reefs around the coast of Phuket, particularly those on the outer reef edge, are currently displaying the highest cover they have ever shown in their 30 year monitoring history (Brown – pers. comm.) which may simply be a feature of steadily rising sea levels. There has also been no major bleaching and mortality since 1995 at these sites and the generally good status of these shallow reefs is also reflected at regularly monitored sub-tidal reef locations on the western coast of Thailand where reef condition is reported to have improved over recent years (Wilkinson, 2008). A recent survey of coral disease in Thai waters revealed a very low incidence of disease compared to that noted in the Caribbean and Great Barrier Reef (Kenkel, 2008).

## Summary

While the steadily rising sea temperature may be exerting an effect on coral growth rates of corals in the Andaman Sea it does appear that their history of exposure to physical rigours and resultant robust physiology may enhance their resistance to climate change. These factors, coupled with oceanographic features such as dynamic water circulation and reduced temperatures/light at critical times of the year, could lead to these turbid reefs being protected from some of the most imminent effects of global warming though the most recent mass bleaching of corals in May 2010 will prove a severe challenge to the resilience capabilities of these reefs.

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## Cross-references

[Coral Reefs of India](#)  
[Indian Ocean Reefs](#)  
[Tsunami](#)

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## EASTERN TROPICAL PACIFIC CORAL REEFS

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## Introduction

### Background

In his coral reef book of 1842, Charles Darwin indicated that there were no coral reefs in the Eastern Tropical Pacific (ETP). Afterward, reef-building corals from the region were described (e.g., Verrill, 1870; Pourtalès, 1875; Crossland, 1927; Durham and Barnard, 1952; Durham, 1966), but the idea that there were no coral reefs in the region persisted (Stoddart, 1969) until the early 1970s when Peter W. Glynn documented coral reefs in Panamá (Glynn et al., 1972), Colombia (Glynn et al., 1982), Galápagos (Glynn and Wellington, 1983), and Costa Rica (Glynn et al., 1983). We now know that coral reefs are present in the region and many have been described, including those from México (Reyes-Bonilla, 2003), Clipperton Atoll (Glynn et al., 1996), El Salvador (Reyes-Bonilla and Barraza, 2003), Costa Rica (Cortés and Jiménez, 2003), Panamá (Maté, 2003), Colombia (Zapata and Vargas-Angel, 2003), and Ecuador (Glynn, 2003). Recently, the coral reefs of Pacific Nicaragua were studied and extensive areas located (J.J. Alvarado, personal communication 2009).

The ETP extends from the southern end of the Gulf of California, México (~23–25°N) to the Gulf of Guayaquil, Ecuador (~2–4°S) (Reyes-Bonilla, 2003; Glynn, 2003; Robertson and Cramer, 2009) (Figure 1). The region comprises eight countries with coral reefs: México, France, El Salvador, Nicaragua, Costa Rica, Panamá, Colombia, and Ecuador. The ETP has been divided into several biogeographic provinces (see review in Robertson and Cramer, 2009). Glynn and Ault (2000) divide the region into three reef-coral provinces: (1) equatorial – mainland Costa Rica to Ecuador, including the oceanic islands of Coco and Galápagos; (2) northern – mainland México and the Revillagigedo Islands; and (3) the island group – Malpelo Island and Clipperton Atoll in the ETP, and Johnston and Fanning islands in Hawaii. Based on the fish fauna, Robertson and Cramer (2009) divide the ETP into two coastal biogeographic provinces: (1) Cortez (Gulf of California and southern end of the Baja Peninsula); and (2) Panamic (central México to Ecuador); and one oceanic province, Ocean Islands: the Revillagigedo group, Clipperton Atoll, Isla del Coco, Isla Malpelo, and the Galápagos Islands. For most groups of organisms, the peak of species richness is the central Panamic province, Costa Rica, and Panamá (Guzman et al., 2004; Robertson and Cramer, 2009; Wehrtmann et al., 2009).

Coral reefs of the ETP are relatively small, discontinuous, and built by a few coral species but have a high diversity, complex food webs, and a long growth history (Guzmán and Cortés, 1993; Cortés, 1997; Glynn, 2004). They are the minimum expression of a coral reef (Cortés, 1997). In this section, I will describe the coral reefs of the ETP, starting with the climate and oceanographic setting, followed by the growth history of reefs in the region, modern-day reefs, and the main threats.

## Physical environment

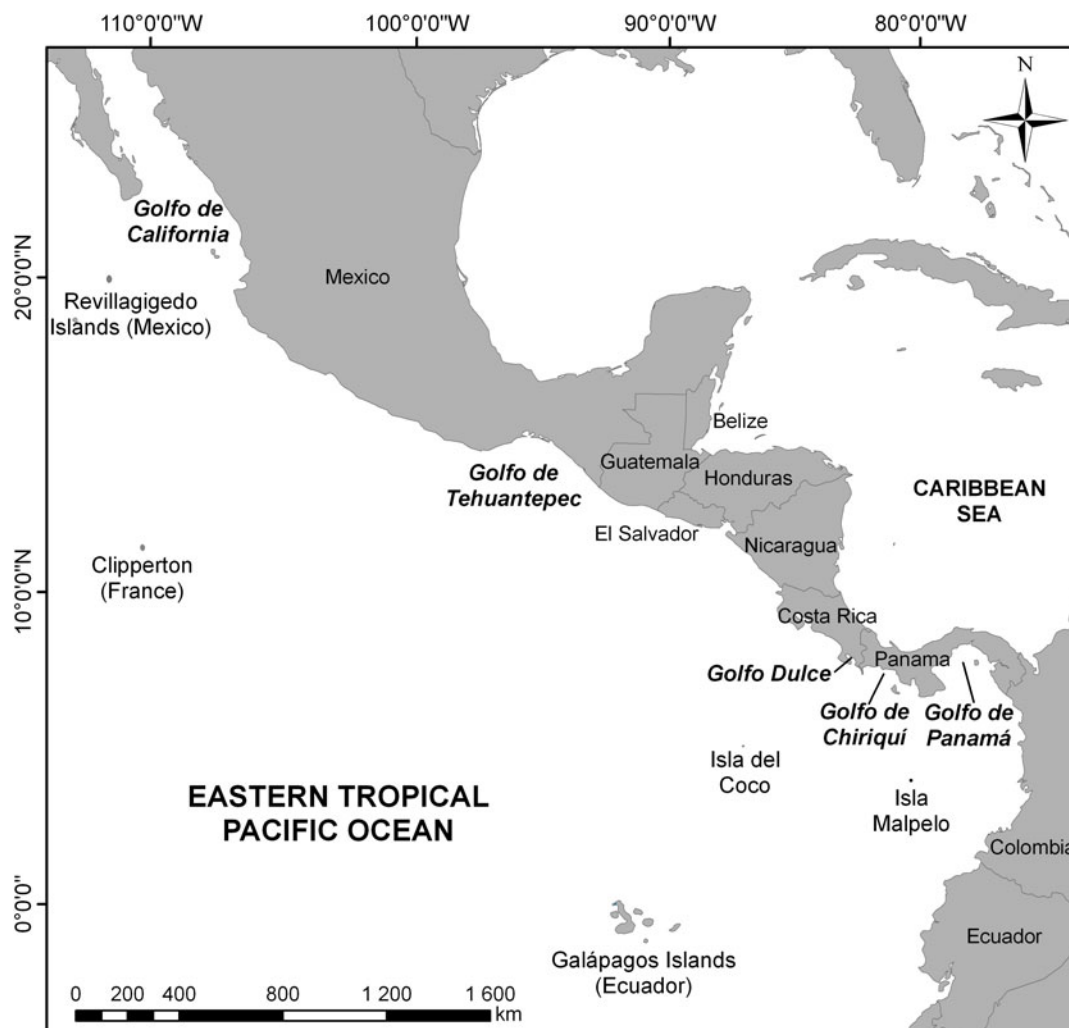
### Climate

In the ETP the climate is controlled mainly by the north–south displacement of the Inter-Tropical Convergence Zone (ITCZ), a low-pressure belt just north of the equator (Alfaro, 2002; Amador et al., 2006; Alfaro, 2008). The coast of the Americas along the ETP are characterized by dry regions from México to northern Costa Rica and by wet to very wet climates from there to southern Ecuador (Taylor and Alfaro, 2005). Off-shore regions north of 10°N and south of 2°N are dry, and the oceanic islands arid. Within this region, the ITCZ moves north and south carrying high precipitations, and at around 5°N is Isla del Coco, the only oceanic island in the region with lush tropical forest (Garrison, 2005; Alfaro, 2008). The dry season in the northern ETP extends from December to April–May and it is due to the southward displacement of the ITCZ (Alfaro, 2002; Taylor and Alfaro, 2005; Amador et al., 2006).

### Hydrography

The main currents in the ETP are responsible for the prevailing oceanographic conditions and transport of





**Eastern Tropical Pacific Coral Reefs, Figure 1** Eastern Tropical Pacific coral reefs region.

organisms in the region. The strongest is the Equatorial Current, which transports waters from the eastern to the western side of the Pacific Ocean; north and south of this current are the Counter Currents, with the North Equatorial Counter Current (NECC) being the most important (Fiedler and Talley, 2006; Kessler, 2006; Lizano, 2008). The NECC is primarily responsible for the presence of Western Pacific coral species in the ETP (Cortés, 1986; Glynn and Ault, 2000).

The ETP is bounded by the California Current to the north and the Humboldt Current (aka Perú–Chile Current) to the south. Important currents within the region are the Costa Rica Current which flows along Central America from southern Costa Rica north to Mexico, bridging the Central American gap, between El Salvador and Mexico (Badan-Dangon, 1998; Kessler, 2006). The other current is the one flowing from the Panama Bight to the Galápagos Island (Rodríguez-Rubio et al., 2003; Kessler, 2006).

Environmental conditions of the central ETP are structured by the Eastern Pacific Warm Pool, a water mass characterized by high temperatures of around 27–28°C year round (Fiedler and Talley, 2006). Seasonal upwellings occur in the region, primarily at three areas where the Mesoamerican Isthmus has a low profile (Tehuantepec, México; Gulf of Papagayo, Costa Rica–Nicaragua; and Gulf of Panama, Panamá), and the Trade Winds blow across from the Intra-Americas Seas (Gulf of Mexico and Caribbean) (Alfaro and Lizano, 2001; Amador et al., 2006; Willet et al., 2006). Eddies, 150–500 km in diameter, are formed where the strong wind jets flow across the low altitude sections of Mesoamerica (Amador et al., 2006; Willet et al., 2006).

The ETP has a shallow and well-defined thermocline that ranges from 30 to 50 m depending on the region. There is also a thick oxygen-minimum layer between 300 and 700 m depth, especially around the continental shelf, where oxygen concentrations can range from near

zero to 0.5 ml of O<sub>2</sub> per liter of seawater, or <45 µmol/kg (Helly and Levin, 2004; Fiedler and Talley, 2006; Stramma et al., 2008). The pH of the region is lower compared to other tropical regions (Feely et al., 2004; Orr et al., 2005; Kleypas et al., 2006), especially during the seasonal upwellings.

El Niño-Southern Oscillation (ENSO) is an ocean-atmosphere phenomenon generated in the Eastern Pacific, with significant climatic and economic impacts worldwide (Glantz, 2001). During an ENSO event, the water temperature of the ETP rises, resulting in some cases, especially in the last two decades, in the mass mortality of corals and other marine organisms (Enfield, 1989; Glynn, 1990; Wang and Fiedler, 2006).

In summary, the ocean dynamics of the ETP depend on the large-scale ocean circulation with seasonal modifications due to wind variations and the displacement of the ITCZ. On a longer time scale, ENSO events play a significant role in the ocean dynamics and distribution of the biota of the ETP (Fiedler and Talley, 2006; Wang and Fiedler, 2006; Lizano, 2008).

## Coral reefs

### Geological history

The geological history of ETP coral reefs started after the closure of the Central American Isthmus some three million years ago (Coates et al., 1992). Before that, the waters of what is now the ETP were connected to the present day Caribbean Sea, sharing flora and fauna (Stehli and Webb, 1985; D'Croz and Robertson, 1997). The ETP is now one of the most isolated ocean regions of the world, separated from the Central Pacific by the East Pacific Barrier. This vast expanse of deep water has been an effective barrier to dispersal of tropical shallow-water organisms throughout the Cenozoic (Cortés, 1986; Grigg and Hey, 1992; Glynn and Ault, 2000). The main currents in the ETP are from east to west, the north and south Equatorial Currents (Glynn et al., 1996; Fiedler and Talley, 2006; Lizano, 2008). However, the weaker but nevertheless important North Equatorial Countercurrent can transport organisms to the Eastern Pacific from the Central and Western Pacific (Scheltema, 1988; Richmond, 1990; Glynn et al., 1996).

After the closure of the Central American Seaway, all Caribbean reef-building corals in the ETP became extinct and were substituted by Indo-Pacific species (Dana, 1975; Cortés, 1986; Glynn, 1997). At present, there are five genera shared but not a single species of reef-building corals in common between the Caribbean and the ETP (Cortés, 2003). Other marine groups in the ETP also show this Indo-Pacific affinity, including mollusks (Scheltema, 1988), echinoderms (Lessios et al., 1998), and fishes (Robertson and Cramer, 2009).

With the closure of the Central American Seaway, oceanographic conditions profoundly changed in the ETP (D'Croz and Robertson, 1997). Now, El Niño could develop bringing warm waters to the region (Enfield, 1989), and the seasonal upwellings off the low lands of

Mesoamerica bring cold waters to the region (Glynn et al., 1983; Willet et al., 2006). The ETP is also a pocket of low-salinity and low-pH waters as compared to other oceans (Fiedler and Talley, 2006; Kleypas et al., 2006; Lizano, 2008). All these conditions are inimical for reef development and consolidation (Cortés, 1997; Manzello et al., 2008). Additionally, there were significant changes to oceanic circulation with the closure of the Central American Isthmus.

The continental shelves of ETP are narrow and drop abruptly to a deep seafloor with some seamounts and ridges (e.g., Carnegie and Cocos). The narrowness of the shelf contributes to the limited development of coral reefs in the region. Cortés (1986) suggested that during the low sea level stands in the Holocene significantly reduced the area where coral reefs could develop. This, combined with the changing oceanographic conditions in the ETP after the closure of the Central America Seaway, resulted in the elimination of most coral reefs in the region and allowed subsequent replenishment from the Western Pacific.

### Holocene growth history

Extant coral reef growth in the ETP started around 5,600 years BP (Glynn and Macintyre, 1977; Cortés et al., 1994). In Panamá, the dominant reef-framework builders are pocilloporid corals, mainly *Pocillopora damicornis*. Reef growth ranges from 1.3 to 4.2 m/1,000 years in the reef flat to 7.5 m/1,000 years in the reef front. Mean maximum reef thickness was higher in the non-upwelling region (Gulf of Chiriquí: 8.3 m, with a maximum of 13 m) than in the upwelling Gulf of Panama (4.2 m) (Glynn and Macintyre, 1977).

At Punta Islotes in Golfo Dulce, Costa Rica, the initial phase of reef growth was by pocilloporids, which created a substrate over sandy bottoms on which *Porites lobata* grew, the dominant reef-frame builder in this location. During the first 3,000 years, growth was slow, but between 2,500 and 500 year BP reef structure growth was extremely fast, in the order of 5–8.3 m/1,000 years, attaining reef framework thickness of up to 9 m (Cortés et al., 1994). At around 500 year BP, there was a significant increase in fresh water in Golfo Dulce. Tectonic movements altered the watersheds, and two large rivers started flowing into the inner section of the gulf where the reefs were growing (Cortés, 1990). This slowed reef accretion, and about 60 years ago reef growth completely stopped when there was an increase in terrigenous sedimentation as a result of the removal of the forest for banana plantations. Sediments loads are still high due to deforestation, inappropriate agricultural practices, coastal alteration, and road construction in the gulf's watershed.

Coral reef growth off the coasts of Panamá and Costa Rica has resulted in thick reef structures (up to 13 m), while in offshore islands (Isla del Caño and Isla del Coco, Costa Rica; and the Galápagos Islands, Ecuador) the reef framework is only a thin veneer of corals over

non-carbonate substrates (Macintyre et al., 1992). The relief of the reef structure is inherited from the non-carbonate substrate, with some large massive corals present. At Isla del Caño, the oldest framework was 2,000 year BP, while at Isla del Coco and the Galápagos Islands samples from the base of the largest *Porites* colonies yield dates of between 320 and 450 years BP (Macintyre et al., 1992).

Postdepositional alteration of corals is minimal in the ETP (Glynn and Macintyre, 1977; Cortés et al., 1994), as is subsequent reef consolidation (Cortés, 1997; Manzello et al., 2008). This may be due to the rapid accumulation rates, lack of high turbulence, and, in general, low pH of the surrounding waters (Glynn and Macintyre, 1977; Cortés, 1997; Manzello et al., 2008). These reefs are subject to rapid bioerosion (Cortés, 1997; Fonseca et al., 2006), resulting in very few examples of exposed Holocene reefs (Glynn and Wellington, 1983; Denyer and Cortés, 2001). ETP reefs are very fragile and, in general, are obliterated before preservation (Cortés, 1993). Branching corals are uncemented, and massive colonies are usually highly bioeroded and in many places unattached to the substrate (Scott and Risk, 1988; Fonseca, 1999). Reef framework is also bioeroded, especially once the coral dies (Glynn et al., 1979; Glynn, 1988; Colgan, 1990; Glynn and Colgan, 1992; Eakin, 1996; Reaka-Kudla et al., 1996; Fonseca et al., 2006). In conclusion, reef preservation is very low in the ETP (Cortés, 1997).

### Types of coral reefs

There are at least 35 species of zooxanthellate corals in the ETP (Reyes-Bonilla, 2002), but only three are important reef builders across the entire region (*Pocillopora damicornis*, *P. elegans* and *Porites lobata*). *Pocillopora* spp. reefs are found in México (Reyes-Bonilla, 2003), Costa Rica (Cortés, 1996/1997; Cortés and Jiménez, 2003), Panamá (Maté, 2003; Guzman et al., 2004, 2008), Colombia (Glynn et al., 1982; Zapata and Vargas-Ángel, 2003), and the Galápagos Islands (Glynn and Wellington, 1983; Glynn, 2003). *Porites* reefs are found at Clipperton Atoll (Glynn et al., 1996), in Costa Rica (Cortés and Jiménez, 2003), and in some areas of the Galápagos Islands (Glynn and Wellington, 1983; Glynn, 2003). Other species that are important as reef builders in particular localities are *Pocillopora eydouxi* in Colombia (Glynn et al., 1982), Panamá (Guzmán et al., 1991), and Costa Rica (Cortés, 1996/1997); and *Pavona clavus*, *Psammocora stellata*, and *Leptoseris papyracea* in Costa Rica (Cortés, 1990; Jiménez, 2001; Bezy et al., 2006).

Coral communities that increase structural heterogeneity on sand/rubble or rocky surfaces are very important in the ETP. In some areas, they may be important contributors to the local benthic ecology of non-reefal habitats. These coral communities can be formed by scattered colonies of the main reef builders growing over basalts or sand/rubble, as in Bahía Culebra, Costa Rica (Jiménez, 2001), or by non-reef-building corals, e.g., *Diadema*

*distorta* and *Psammocora stellata* in deep reefs in the Galápagos Islands (Feingold, 1995, 1996); and *Diadema distorta* and *Porites sverdrupi* in the Gulf of California (Feingold et al., 2009).

In many regions, the predominant reef builders in shallow waters are pocilloporids, while in deeper waters the main reef builders are *Porites lobata* and *Pavona* spp., for example, in Panamá (Glynn et al., 1972), Galápagos Islands (Glynn and Wellington, 1983), and Costa Rica (Guzman and Cortés, 1989; Cortés, 1990; Guzman and Cortés, 2007). The shallow reefs in the ETP are physically controlled by wave action and low tidal exposure, while deeper sections are biologically controlled mainly by predation and competition (Glynn, 1976; Guzman and Cortés, 1989).

### Threats/impacts

#### El Niño-Southern Oscillation (ENSO)

ENSO events are atmospheric-oceanographic phenomena which in the ETP manifest themselves as warming episodes with devastating consequences to corals and coral reefs (Glynn, 2000). These warming events have caused the most damage to coral reefs in the entire ETP. The first major recorded event was during the 1982–83 El Niño, causing coral mortalities ranging from 50 to 99% (Glynn, 1984). Glynn et al. (1988) determined that the greater the temperature anomaly, the longer the warming event, and the faster the warming increased, the more was the impact on the coral communities and reefs. Subsequent warming events associated with ENSO, especially the 1997–1998 event, also caused significant impacts (Glynn and Colley, 2001). All regions of the ETP have been affected: México (Reyes-Bonilla, 2003), Costa Rica (Guzman and Cortés, 2001; Jiménez and Cortés, 2001; Jiménez et al., 2001; Jiménez and Cortés, 2003; Guzman and Cortés, 2007), Panamá (Glynn, 1990; Maté, 2003), Galápagos, and mainland Ecuador (Glynn, 2003). Recovery has been observed in some areas but it has been slow (Guzman and Cortés, 2001; Guzman and Cortés, 2007).

#### Subaerial exposure

Extreme low tides have been observed in the ETP and have limited local effects, but significant for reef flats depending on the season and time of day. These exposures of the shallow reef may be due to extremely low astronomical tides and ENSO-related sea-level drop (Glynn, 1984; Eakin and Glynn, 1996). Exposure of corals have been illustrated from Panama (Eakin and Glynn, 1996; Maté, 2003) and Ecuador (Glynn, 2003).

#### Sedimentation

The presence of terrigenous sedimentation in coral reefs is a major cause of reef deterioration worldwide (Fabricius, 2005). Excessive amounts will bury and kill corals, while low concentrations also have negative effects. The corals must spend energy to clean themselves by ciliary action, polyp expansion, and/or mucus sheet production all with



an energy cost – energy that cannot be used for growth, reproduction, resistance to diseases, or wound repair (Cortés and Risk, 1985; Rogers, 1990; Fabricius, 2005).

In the ETP, the impact of sediments have been studied in Mexico (Ochoa-López et al., 1998; Granja-Fernández and López-Pérez, 2008), Costa Rica (Cortés, 1990; Alvarado et al., 2009), Colombia (Zapata and Vargas-Ángel, 2003), and Ecuador mainland (Glynn, 2003). In some areas, for example, Golfo Dulce in southern Costa Rica, terrigenous sedimentation resulted in the cessation of reef growth (Cortés et al., 1994).

### Organism extraction

The impact of reef organisms extraction has not been studied in detail. In several countries in the region ornamental fishes are extracted for the aquarium trade with no or very limited control (McCauley et al., 2008; <http://www.aquariumcouncil.org>). Corals and octocorals are also extracted for the curio trade in El Salvador (personal observation), Costa Rica (Cortés and Murillo, 1985), Colombia (Zapata and Vargas-Ángel, 2003), and Ecuador (Glynn, 2003). Panama is the only country in the region with laws that prohibit the extraction of live or dead coral (Maté, 2003), as is also in the Galápagos Islands (J. S. Feingold, personal communication).

### Climate change

Climate change is now considered one of the main threats to coral reefs worldwide (Hughes et al., 2003; Hoegh-Guldberg et al., 2007; Hughes et al., 2007; Baker et al., 2008). Sea water warming and associated bleaching is the most obvious impact on corals reefs, resulting in reduction in growth rates, reproductive output, recruitment/survivorship of larvae, competitive abilities, capacity to regenerate tissue, increased susceptibility to diseases/stress, and partial/total mortality of the colony. There can also be changes in the structure and functioning of coral populations and reef communities, and phase shifts to different group/species community composition (Baker et al., 2008; McClanahan et al., 2008). A not so obvious consequence of the accumulation of CO<sub>2</sub> in the atmosphere is ocean acidification (Kleypas et al., 2006; Hoegh-Guldberg et al., 2007), and this may be the main threat to the existence of coral reefs in the future. This problem is especially exacerbated in the ETP, since pH in the region is lower than other oceans, and drops even more during the upwelling periods.

### Coral reef resilience

Resilience is generally defined as the ability of a coral reef to return to a previous state after some perturbation (West and Salm, 2003; Nyström et al., 2008). Several characteristics of coral reefs are recognized as important to maximized resilience: these include maintaining a healthy herbivore community, high biodiversity, inter-reef and inter-system connectivity, and reduced human impact (Hughes et al., 2005; Mumby and Hastings, 2008;

Nyström et al., 2008). Speed of recovery and resilience of coral reefs is greater in areas with less human activity.

### Conclusions

ETP coral reefs are constructed by just a few species of reef-building corals, yet they are highly complex in interspecies interactions (Cortés, 1997; Glynn, 2004). As carbonate structures, they started growing shortly after rising sea level flooded appropriate substrates over 5,000 years ago, but the frameworks are fragile, with little cementation, and are easily bioeroded. For this reason, there are practically no examples of exposed Holocene fossil reefs in the region as is so common on the Caribbean. These coral reefs are widely distributed from southern Baja California to Ecuador, including offshore islands, with a similar suite of reef-building corals (*Pocillopora* spp., *Porites lobata* and *Pavona* spp.), even though they range from extreme dry regions to very humid and from upwelling to nonupwelling areas. The main impact on ETP coral reefs have been El Niño warming events; other disturbances include cooling events, subaerial exposure, excessive terrigenous sedimentation, organisms extraction, and climate change, among others. The corals in this region were significantly impacted by the 1982/83 El Niño and then again by the 1997/98 event, but most reefs are recovering, though slowly. Coral reef resilience must be maximized by maintaining a healthy herbivore community, high biodiversity, inter-reef and inter-systems connectivity, and reduced human impact.

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## Cross-references

[Bioherms and Biostromes](#)  
[Coral Bleaching](#)  
[Coral Cay Classification and Evolution](#)  
[Corals: Environmental Controls on Growth](#)  
[Diagenesis](#)  
[El Niño, La Niña, and ENSO](#)  
[Fringing Reefs](#)  
[General Evolution of Carbonate Reefs](#)  
[Global Ocean Circulation and Coral Reefs](#)  
[Holocene Reefs: Thickness and Characteristics](#)  
[Impacts of Sediment on Coral Reefs](#)  
[Ocean Acidification, Effects on Calcification](#)  
[Temperature Change: Bleaching](#)  
[Upwelling and Coral Reefs](#)

## ECHINODERMATA

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## Definition

Echinodermata is defined as a phylum of marine invertebrates with a spiny skin and radial symmetry.

## Introduction

Echinoderms are a conspicuous and diverse component of the invertebrate fauna of coral reefs and include

species from five extant classes Asteroidea (sea stars), Ophiuroidea (brittlestars), Echinoidea (sea urchins), Holothuroidea (sea cucumbers), and Crinoidea (feather stars). They have a distinct radial symmetry based on pentamery. There are usually five radii (e.g., arms of sea stars), although multiarmed (6+ arms) asteroids and brittle stars are common. Asteroids are star shaped with the arms (five or more) tapering from the disc (e.g., *Linckia*) or a cushion-like pentagon shape lacking arms (e.g., *Culcita*). Ophiuroids have a round central disc and slender flexible arms that are sharply set-off from the body. Their body can have a simple (brittle stars or serpent stars) or branched (basket stars) profile. Echinoids have a rigid globose body covered by spines. Holothuroids are elongate sausage-shaped. Crinoids have an array of feather-like arms that range in number from five to more than two hundred.

Echinoderms are an ecologically important component of coral reef ecosystems. They are often the dominant organisms on the sea floor. In shallow and intertidal coral reef environments, this is particularly true of sea cucumbers (e.g., *Holothuria*) on reef flats and sandy areas. Several ecologically important keystone echinoderm species exhibit boom and bust cycles in population density, including sea urchins (*Diadema*) and the crown of thorns sea star (*Acanthaster planci*) (see section). Echinoderms provide crucial ecological services to reef systems, with roles in nutrient cycling, predation, water quality regulation, and herbivory.

Most tropical sea cucumbers are benthic deposit feeders in soft sediment inter-reefal and lagoon environments, where they provide important ecosystem services. They enhance the productivity of nutrient poor carbonate sediments through their bioturbation, burrowing, and feeding/digestive activity. Taxonomically, these sea cucumbers have long been a challenge, a problem of concern for the management of poorly known commercial beche de mer species, many of which are now locally extinct due to overfishing.

Most sea urchins are grazers using their hard teeth to remove algae and encrusting organisms from the surface. As a member of the grazing guild on coral reefs, sea urchins contribute to keeping the biomass of algae low, thereby preventing the overgrowth of algae over coral substrate. Loss of urchins, such as the disappearance of *Diadema* in the Caribbean in the 1980s, resulted in an ecological shift from coral to algal dominated reefs. *Tripteneustes gratilla* a commercially important tropical sea urchin is a specialist on sea grass. The burrowing activity of echinoids, particularly *Echinometra* species, is important in bioerosion of coral reef and intertidal habitats.

Crinoids and many ophiuroids are suspension feeders extending their arms above the substrate to capture food particles on their small tube feet that line the arms. The food is captured from flow, and so they take up positions on the reef to take advantage of ambient water movement.

Food particles are conveyed to the mouth in the centre of the disc by food tracts. Some ophiuroids are predators and scavengers.

## Conclusion

Echinoderms are key members of the biodiversity of coral reef ecosystems. Some species, such as *Acanthaster*, *Diadema*, and *Echinometra*, are particularly important in structuring coral reef communities. Some sea urchins and many sea cucumbers are important as fishery species.

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## Cross-references

[Acanthaster Planci](#)

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## ECO-MORPHODYNAMICS

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## Definition

Eco-morphodynamics is the interaction and co-adjustment of coral reef structure, morphology, and physical hydrodynamic and ecological processes that is mediated by the production, transfer, and deposition of calcium carbonate.

## Introduction

Coral reefs and reef sedimentary landforms are unique in that they are composed predominantly of calcium carbonate (CaCO<sub>3</sub>) that is generated almost entirely from ecological processes. Reef scientists have long recognized the fact that the structure of coral reefs reflects a balance between the constructive processes of framework building corals and other primary and secondary carbonate

producers, and the destructive processes of mechanical wave action and bioerosion (e.g., Darwin, 1842; Scoffin, 1992). Initially, the recognition of these dynamics underpinned explanations of the presence and gross structure of coral reefs and they have been modeled using a carbonate budget approach (Perry and Hepburn, 2008; Perry et al., 2008). The by-products of reef growth and destruction (detrital sediment) can also lead to landform construction and change. For instance, reef islands rely on production and transfer of detrital sediment from a contiguous reef system, although they have typically been regarded as losses to the reef sediment budget (Scoffin et al., 1980; Hubbard et al., 1990; Kleypas et al., 2001). Over the past century, an expansion of research to describe and account for other morphological features on and adjacent to coral reef structures has recognized that the balance of constructive and destructive processes on reefs operates at a range of space and time scales. Variability in that balance (e.g., in extent, rates, duration, timing) produces a wide range of macro- to micro-scale geomorphic units, from entire reef platforms to a particular spur and groove morphology.

Physical processes that mechanically erode, transport, and deposit calcium carbonate are of paramount importance in controlling the distribution, structure, and morphology of reefs and sedimentary landforms (Scoffin et al., 1980). Once a reef is constructed, feedbacks that modify microenvironments and process interactions that drive the distribution of ecological communities and morphological products exist. The term “eco-morphodynamics” was recently introduced by Kench et al. (2009) as a conceptual framework to provide a more detailed exploration of the complex relationships that exist between ecological and physical processes and reef geomorphology.

### Morphodynamic origins

Eco-morphodynamics is an extension of the morphodynamic concept, which has been widely used by geomorphologists to account for the co-adjustment of landforms and processes in coastal environments (Wright and Thom, 1977; Cowell and Thom, 1994). Typically applied in siliciclastic coastal settings, a morphodynamic approach accounts for hydrodynamic processes and their interaction with seafloor and coastal features to drive morphological adjustment involving the movement of sediment. Hydrodynamic processes include waves, tides, and wind-induced currents. While these processes respond instantaneously to morphology, morphological change itself is slower, requiring the redistribution of sediment. As sediment takes a finite time to move, there is a lag in the morphological response to hydrodynamic forcing. Therefore, sediment can be considered to be a time-dependent coupling mechanism. Unique to coral reef systems, the sediment reservoir is produced solely by ecological processes that produce calcium carbonate. Furthermore, different coral reef settings (locations; geomorphic

zones) vary greatly in the rates at which they produce calcium carbonate (Kinsey, 1983). Consequently, the carbonate factory is a highly space- and time-dependent coupling mechanism. However, the time dependency of reef geomorphology to the carbonate factory emerges not only from the temporal lags in redistribution of material but also from the timeframes associated with organism growth, mortality, and conversion to detrital sediment (Perry et al., 2008). The influence of such temporal lags on morphological change in reef systems is poorly understood.

### Eco-morphodynamic framework

The structure and function of the eco-morphodynamic framework of a coral reef system is presented in Figure 1, which clearly shows the importance of carbonate cycling. Examination of this framework highlights a number of implications for the co-adjustment of physical processes, reef ecological communities, and geomorphic products.

### Boundary controls

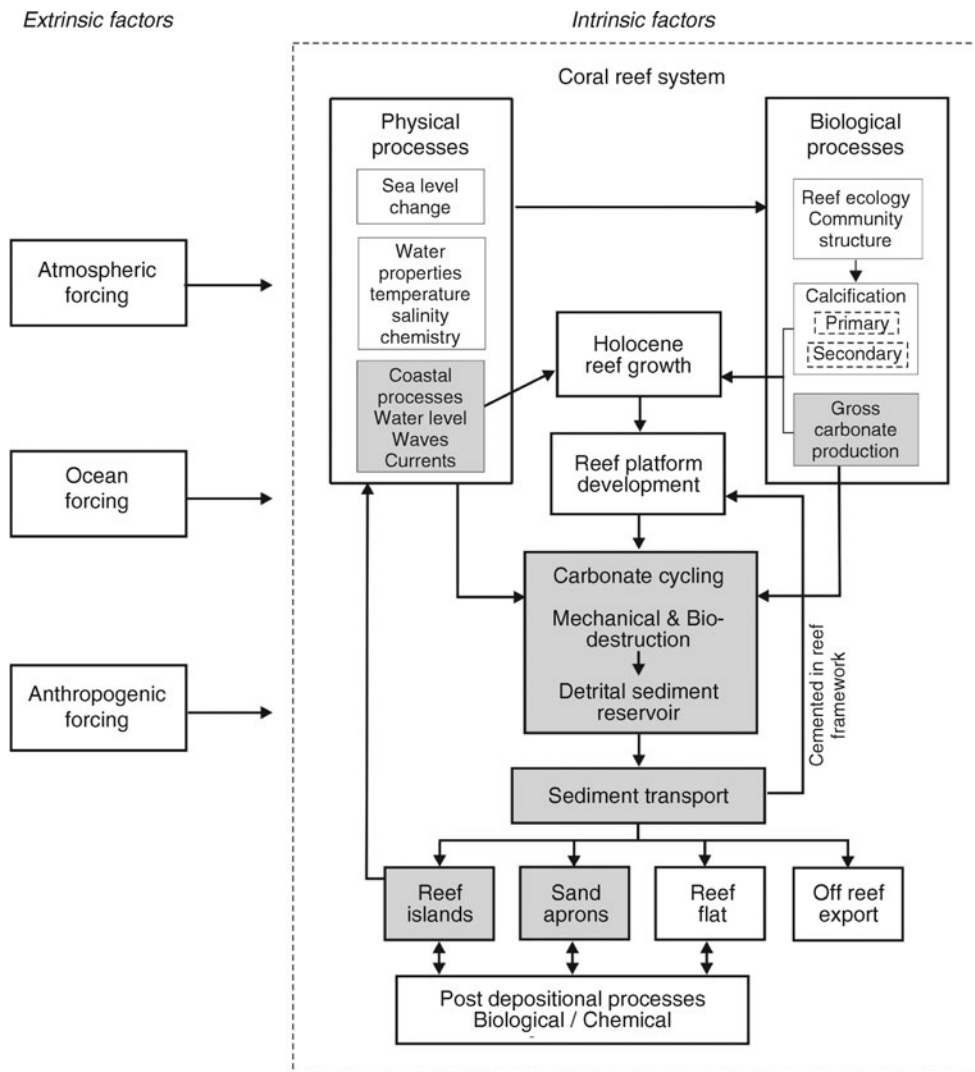
Alterations in boundary controls will force change in coral reef system state (ecological, physical, and geological characteristics). Such changes in boundary conditions can occur as a consequence of extrinsic changes in the atmosphere–ocean system such as sea-level rise, ocean temperature, and chemistry variations (Hoegh-Guldberg, 1999; Kleypas et al., 2001; Buddemeier et al., 2004; Orr et al., 2005; Kench et al., 2009). Changes in the intrinsic factors (e.g., physical and ecological processes) can also force dynamic change in reef systems. These intrinsic linkages are themselves impacted by anthropogenic activities such as over-exploitation of physical and biological resources and coastal construction (Browne and Dunne, 1988; Jackson, 2001; Hughes et al., 2003; Lidz and Hallock, 2000; Sheppard et al., 2005).

### Time and space scales of change

The magnitude, mode, and timeframes of change (responsiveness) in the system are likely to vary considerably between different components of a reef system. Examples include the following:

- (i) Development of coral reef platforms, which are known to be modulated by sea-level oscillations at millennial timescales (Kennedy and Woodroffe, 2002; Montaggioni, 2005)
- (ii) Reef island development, which is a function of a reef basement, sediment supply, and process regime, occurring at centennial timescales (Woodroffe, 2003; Kench et al., 2005)
- (iii) Shoreline dynamics of reef islands, which occur at event to decadal timescales in response to alterations in wave energy input (Maragos et al., 1973; Flood, 1986; Kench and Brander, 2006a)
- (iv) Ecological transitions that can occur at event to decadal timeframes in response to extreme climatic events or changes in ocean temperature, ocean





**Eco-Morphodynamics, Figure 1** Structure and function of the eco-morphodynamic model for the coral reef system. The model shows co-adjustment of biological and physical processes, and coral reef morphology and reef sedimentary landforms that operate at a range of timescales. *Gray shaded boxes* and *dark arrows* highlight linkages between the contemporary eco-morphodynamic systems controlling sedimentary landform development at event- to centennial scales, which are embedded in the broader morphodynamic system that controls coral reef development at centennial to millennial scales. (After Kench et al. [2009]).

chemistry, or water quality (Woodley et al., 1981; Done, 1992; Hughes et al., 1994; Eakin, 1996)

### Feedbacks

There are eco-morphodynamic feedbacks that are temporally specific and those that cascade across timescales. Both provide a degree of self-organization to geomorphic development. For instance, at millennial timescales sea-level change controls the patterning of reef growth. In turn, the reef structure modulates wave and current processes (Gourlay, 1988; Symonds et al., 1995; Kench and Brander, 2006b) that govern the structure of ecological

communities (Chappell, 1980; Done, 1982), reef morphology (Yamano et al., 2003), sedimentation processes, and short-term morphological development of reef-associated landforms (Sheppard et al., 2005).

The eco-morphodynamic framework also indicates that feedbacks are non-linear with significant time lags existing for changes to propagate through the geomorphic system. For instance, ecological transitions may occur in response to short-term bleaching episodes, anthropogenic stress or biological disease (Liddell and Ohlhorst, 1993; Eakin, 1996). Depending on the magnitude of change in the ecological system (e.g., the severity and spatial extent of coral mortality and the rate of recolonisation by corals),

the carbonate factory may alter its sediment budget status over decades (Perry et al., 2008). Ultimately, depending on the magnitude and temporal scale of ecological change (persistence or ephemeral transition), alterations in the carbonate budget may, or may not, propagate through the system to yield detectable changes in the geomorphic system at decadal to centennial timeframes (Kench et al., 2009).

## Summary

The formation and morphological adjustment of coral reefs and reef sedimentary landforms results from the dynamic interaction between biological and physical processes, which operate at a range of time and space scales. Eco-morphodynamics is a conceptual framework that identifies the major process response linkages between physical and biological processes which are responsible for the spatial and temporal dynamics of ecological communities, physical processes, and geomorphology (Figure 1). Central to the framework is the importance of the coral reef “carbonate factory” in providing the building blocks (skeletal material, sand, and gravels) for construction of reef landforms. The framework also highlights the multiple extrinsic and intrinsic factors that promote change in ecological, physical, and geomorphic processes and products in reef systems.

Eco-morphodynamics provides a conceptual framework to explore: the sensitivity of landforms to perturbations in boundary conditions; thresholds and timescales of change; and feedbacks, temporal lags, and nonlinearities in the linkages between the physical, ecological, and geological components of reef systems. Currently, these system sensitivities, thresholds, temporal lags, feedbacks, and timescales of relevance to reef geomorphic development and change are poorly resolved.

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## Cross-references

Carbonate Budgets and Reef Framework Accumulation  
Cay Formation  
Climate Change and Coral Reefs  
Corals: Environmental Controls on Growth  
Ecomorphology  
Geomorphic Zonation  
Sea Level Change and Its Effect on Reef Growth  
Sediments, Properties

## ECOMORPHOLOGY

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## Definition

Ecomorphology describes the interrelationship between coral growth form and the dominant environmental factors that influence reefs. It derives from a growth-form response that was suggested by John Chappell in 1980.

## Introduction

A coral reef comprises a limestone substrate across which various organisms are distributed, competing for, and partitioning, space in response to a series of environmental factors, such as light, sediment and wave energy. These factors vary across the reef and represent stresses to which organisms such as the corals respond. The various corals, adopting distinct growth-forms, have discrete tolerances and their distribution appears related to environmental gradients in these stresses. An ecomorphological zonation based on these principles was outlined by Chappell (1980).

## Environmental stresses and their effect on corals

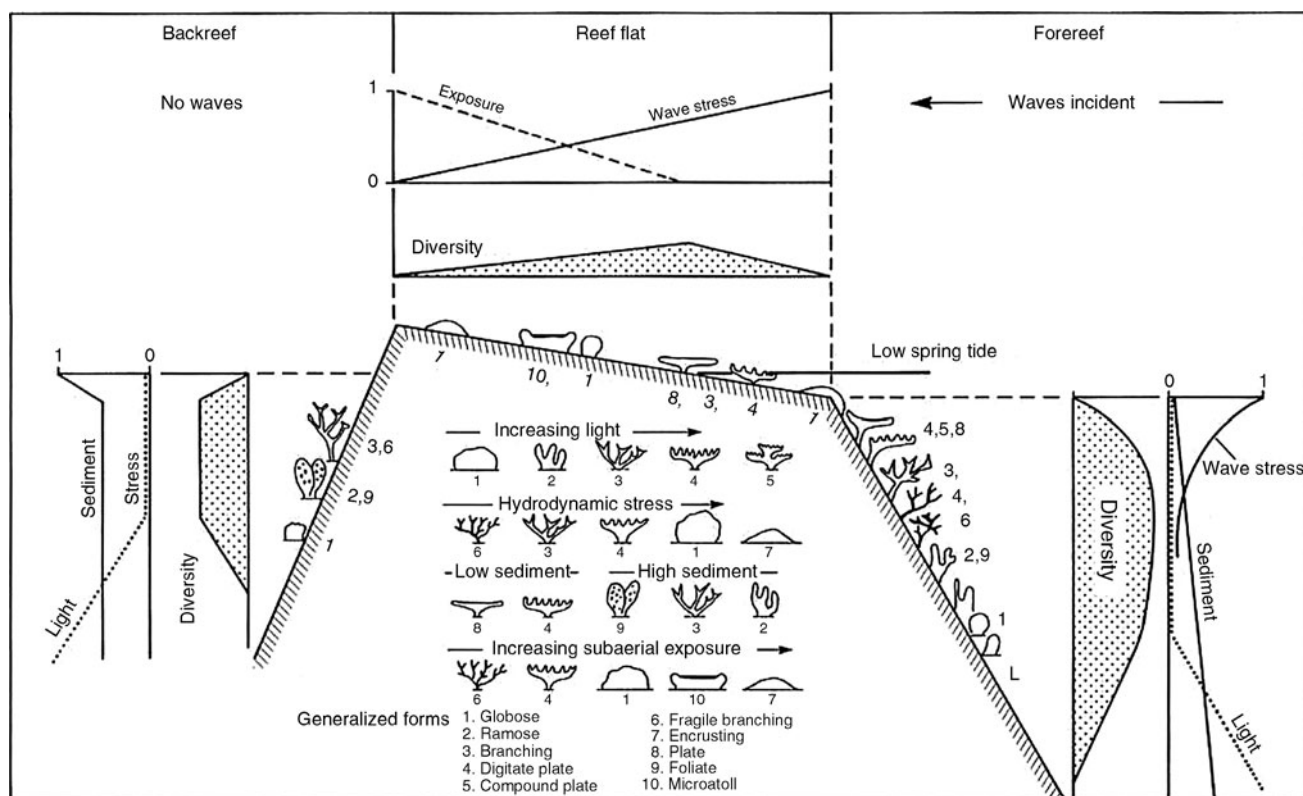
Chappell (1980) hypothesized growth-form responses in corals to four gradients in environmental parameters. Figure 1 is indicative of the sort of responses that he envisaged. (1) Light response: corals require light in order that their symbiotic zooanthellae can photosynthesize, and where light is abundant growth forms can support extensive polyp-covered surfaces in comparison with their projected surface area. Digitate plate and compound plate morphologies can occur near the water surface where light is abundant, being replaced by corals with less polyp-covered surface at greater depth (Figure 1). (2) Hydrodynamic stress: delicate forms of coral are fractured if wave energy is high, and only more robust forms with greater structural strength can persist where wave energy is greatest. (3) Sediment flux effect: although recent research indicates that reefs can support diverse coral communities in some turbid settings, sediment can smother polyps and limit growth. Platy growth forms are more prone to smothering than those that do not have extensive horizontal surfaces. (4) Subaerial exposure: at lowest tides, exposure of coral polyps exerts a stress on corals. Flat-topped microatolls (discoid corals that are living on the margins but dead on top) and encrusting forms are best adapted to such exposure.

## Variation in coral communities across a section of reef

Wave energy is one of the most important controls on reefs and has received considerable study. Corals are often well-developed where wave energy is high, although the most exposed reef crests are generally dominated by coralline algae, often forming a distinct rim. Wave energy is a function of wave height squared and decreases with depth down the reef front. Fragile branching corals are prone to breakage and can only survive where wave energy is low; they are replaced by structurally stronger corals, such as globose or encrusting forms in higher wave-energy settings (Figure 1).

Corals also have to cope with a range of light conditions; for instance, the massive West Indian coral *Montastrea annularis* changes its form, becoming flatter and more platy with depth down a reef front. Platy corals are poorly-adapted to tolerate high sediment loads;





**Ecomorphology, Figure 1** Ecomorphological zonation on a reef, showing characteristic generalized growth forms, in response to light, sediment and wave stress and subaerial exposure (after Chappell, 1980. Reprinted by permission from Macmillan Publishers Ltd: Nature, 1980).

ramose, branching and foliate corals are much better able to cope with high sediment loads and are more common where turbidity is high.

Figure 1 shows a schematic model of coral growth-forms in relation to environmental gradients proposed by Chappell (1980). On the basis of this model growth forms are dominant at different points across the reef profile and hypothetical diversity curves are also derived, ranging from a maximum when environmental stresses are minimal, to zero where any stress is limiting. The reef front is likely to have massive forms at depth. Towards the reef crest more sturdy branching forms of coral will occur, and the branches may be oriented into the dominant wave direction. In the highest wave-energy settings corals will be encrusting, or may be replaced by encrusting coralline algae as occur on the algal ridges of Indo-Pacific reefs.

### Applications of the model

The ecomorphological patterning proposed by Chappell (1980) would suggest that the dominant growth forms of corals vary across reefs. Zonation of organisms has been widely observed on reefs, and such studies formed a basis on which Chappell developed his schema. They also suggest that the processes vary, and of the major environmental factors much research has focused on wave

energy and its variation across reefs. Light is a limiting factor at depth on a reef. At intermediate depths on a reef intricately branching corals can survive, but these are replaced in the zone where waves break by more robust corals, with encrusting forms dominating the reef crest (Hopley, 2008). Subaerial exposure imposes a stress on many reef flats and several coral genera may adopt a microatoll growth morphology as a result of exposure at low tide.

Chappell (1980) considered that this ecomorphological zonation could be used to simulate reef growth, assuming that growth of coral framework is constrained by the four factors such that there is diminished growth as net stress increases and growth ceases when any factor becomes limiting. The model was compared with the overall morphology of fossil reefs on the Huon Peninsula of northern Papua New Guinea, and the taphonomy of coral growth-forms was also an indication of the depth and habitat conditions that had characterized those fossil reefs. The approach has also been found useful for deciphering former habitats in other uplifted Pleistocene reefs on island arcs in the region, and applied in a more restricted way to the less diverse fossil reefs of the Caribbean. The approach has also been of value in interpreting much older fossil reefs, of Cainozoic, Mesozoic and even Paleozoic age, and has been applied in stratigraphic models.

## Summary

Zonation is apparent on many coral reefs and coral growth form reflects environmental gradients in several factors, particularly light availability, wave energy, emersion, and sedimentation patterns.

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## Cross-references

[Corals: Environmental Controls on Growth](#)  
[Eco-Morphodynamics](#)  
[Geister Classification of Reefs](#)  
[Geomorphic Zonation](#)  
[Microatoll](#)  
[Reef Front Wave Energy](#)  
[Sediment Durability](#)

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## EL NIÑO, LA NIÑA, AND ENSO

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## Synonyms

La Niña is also called Anti-El Niño and El Viejo

## Definition

El Niño (The Christ child) is a seasonal current that typically transports warm sea surface water from the Pacific coast of Central America to the equatorial Eastern Pacific. Also, it refers to the migration of Central Pacific equatorial warm water to the east, and the warm phase of the Southern Oscillation.

La Niña (The little girl) is the cool phase of the Southern Oscillation.

El Niño-Southern Oscillation (ENSO) is the coupled ocean-atmospheric shifts in high pressure centers from the equatorial Western Pacific to the equatorial Eastern Pacific.

## Introduction

El Niño, La Niña, and El Niño-Southern Oscillation (ENSO) are related but distinct phenomena. The El Niño current is a seasonal, warm current that typically originates near Central America and flows into sea surface waters off Ecuador and Peru. This current typically appears in late December or early January, and its association with Christmas and the Epiphany led to it being called El Niño (The Christ Child). Central Pacific equatorial warm water that

migrates to the east also produces warming of the Eastern Pacific, and has been called El Niño. The term El Niño is also used to denote the warm phase of ENSO, with La Niña referring to the cool phase (Philander, 1990). ENSO results from a wide scale shift in pressure centers related to feedback cycles within the coupled ocean-atmosphere climate system of the tropical Pacific, potentially influenced by external forcing (Enfield, 1989). During the ENSO warm phase, high atmospheric pressure, typically located in the West Pacific (near Darwin, Australia), shifts to the Central Pacific (near Tahiti), reducing westerly trade wind velocities, and consequently reducing the flow of the South Equatorial Current. Tropical heat that is normally pumped to the west by this current is retained in the Eastern Pacific. Under extreme warm phase ENSO conditions, wind fields reverse and easterly winds move warm surface water into the Eastern Pacific. Kelvin Waves are also associated with Eastern Pacific warming, as they pump subsurface warm water to the east along the equator. Persistence of high pressure in the Central Pacific indicates El Niño conditions, and especially high pressures in the Western Pacific associated with colder Eastern Pacific sea-surface water are indicators of La Niña. The cool phase of ENSO (La Niña) can follow the warm phase as global pressure shifts relax towards normal and occasionally overshoot, resulting in anomalously cool conditions in the eastern tropical Pacific (Enfield, 2001).

Links between ENSO and global climate perturbations have been documented (Holland, 2009), and related impacts to adjacent regions (teleconnections) affect coral ecosystems in the western Caribbean Sea (Coffroth et al., 1990), Indian Ocean (Wilkinson et al., 1999), Indonesia (Brown and Suharsono, 1990), French Polynesia (Hoegh-Guldberg, 1999), and even coral reefs worldwide (Wilkinson, 2000).

ENSO events have occurred every  $3.8 \pm 1.8$  (mean  $\pm$  s.d.) years, and strong and very strong events every  $9.9 \pm 4.2$  years (Enfield and Cid, 1991). No two ENSO events are alike. Their strength is related to the intensity and duration of sea-surface temperature (SST) anomalies (differences between measured temperatures and long-term means). Two very strong events occurred in 1982–1983 and 1997–1998. The event in 1982–1983 was called the strongest of the twentieth century (Kerr, 1983), at least until the 1997–1998 event which was comparable in magnitude (Enfield, 2001). Conditions are now (August 2009) favorable for the development of another ENSO in 2009–2010 (NOAA, 2009).

The strength of the event is generally proportional to the amount of impact to coral. Weak to moderate ENSO events have had little effect, whereas the severe events of 1982–1983 and 1997–1998 resulted in coral mortality ranging from 15 to 99% at locations in the tropical Eastern Pacific (Glynn, 2001).

## ENSO effects on corals

ENSO effects on corals were first well documented during the 1982–1983 event, and even more thorough investigations were performed during the 1997–1998 event

(Glynn, 2001). Sea-surface perturbations associated with the warm phase of ENSO have the strongest effect on corals in the eastern tropical Pacific (Glynn et al., 2001); however, corals in the Central and Western Pacific (Hoegh-Guldberg, 1999), Indian Ocean (Wilkinson, 2000), and Caribbean Sea (Coffroth et al., 1990) are also affected. These perturbations include elevated SSTs, elevated sea level, depressed main thermocline, diminution and reversal of surface and subsurface currents, increased wave assault, decreased nutrients and productivity, and increased rainfall (and concomitant increased sedimentation in nearshore environments) (Philander, 1983; Fiedler et al., 1992). During ENSO cool phase (La Niña), corals in the Eastern Pacific are exposed to opposite conditions; depressed SSTs, lower sea level, elevated main thermocline, intensification of westward-flowing currents, normal wave action, increased nutrients and productivity, and decreased rainfall.

### SST anomalies and coral mortality

Sea-surface warming associated with ENSO is implicated as the primary cause of coral bleaching and mortality (Glynn et al., 1988; Glynn and D'Croz, 1990). Thermal impacts are more related to temperature anomalies (differences from long-term mean temperatures) than absolute temperature. For example, during the 1982–1983 ENSO, mean coral mortality was higher in the Galapagos Islands (99%) than in Costa Rica (51%) even though mean monthly SSTs were lower (28.5 vs. 31°C). Temperature anomalies ranged from +3 to +4°C in the Galapagos Islands where corals were strongly affected, compared to +1 to +2°C in Costa Rica (Glynn, 1990). In the Indian Ocean, temperatures 3–5°C above normal were reported, and mortality up to 90% in shallow habitats was observed (Wilkinson et al., 1999).

Though less well studied, cooling can also stress corals, resulting in mortality. Populations of *Pocillopora* at Devil's Crown, Galapagos Islands, were reduced by approximately 85% following exceptionally cool conditions in 2007 (Feingold, unpublished data). Bleaching and mortality were reported in Costa Rica during cooling associated with a 1985 La Niña event (Guzmán and Cortés, 2001).

Combined effects of ENSO can result in regional-scale extirpation of corals and dramatic change to reef communities. Reductions of corals and subsequent bioerosion of reef framework in the Galapagos Islands have eliminated the few reefs that occurred there (Glynn and Ault, 2000).

### Coral bleaching

ENSO-related coral bleaching occurs when endosymbiotic dinoflagellates (zooxanthellae) either diminish in number within the coral host tissues, or lose their photosynthetic pigment. Since zooxanthellae are an important source of energy, reef-building corals will die unless sufficient populations of the endosymbiont become re-established. Bleaching severity shows species-specific trends, with some corals being sensitive (e.g. *Pocillopora*) and others resistant (e.g. *Psammocora*) (Glynn, 1990). Bleaching

occurs when coral is physiologically stressed, and is most often associated with positive SST anomalies (warming), although other perturbations such as cooling, lower sea level, salinity decrease, and sedimentation contribute.

Bleaching sensitivity is also related to the endosymbiont clade; some zooxanthellae are more tolerant to elevated temperatures than others. For example, in Panama, pocilloporid corals with zooxanthellae in clade D did not bleach, whereas those with clade C did (Baker, 2004). Thus, coral survivors of the 1982–1983 ENSO predominantly harbored clade D endosymbionts, and when these corals were exposed to highly elevated temperatures again in 1997–1998, they were not as severely affected as they were in 1982–1983 (Glynn et al., 2001).

Sea level decrease also results in coral bleaching and mortality, particularly severe when combined with spring low tides. Sea level is low in the west during ENSO warm phase, and low in the east during ENSO cool phase (La Niña). For example, reef flats were exposed in Guam during warm phase ENSO in 1972–1973 (Yamaguchi, 1975), and corals were affected in French Polynesia and the Tokelau Islands during the 1982–1983 and 1993 events (Coffroth et al., 1990). La Niña conditions in 1989 and 1993 resulted in sub-aerial exposure of coral on the reef flat and high coral mortality at Uva Island, Panama (Eakin, 2001).

### Mitigation by depth and light

Coral reefs and coral communities are more common in shallow waters (<10 m depth) where positive temperature anomalies are strongest. However, corals also live in deeper water where sea-surface warming is not so pronounced. In the Eastern Pacific, corals living >15 m in depth were not so strongly affected by ENSO-related warming (0% mortality) as those in shallow waters, due to periodic shoaling of cooler water from the subsurface mixed layer (Feingold, 1996). Wilkinson et al. (1999) reported less coral mortality at depths >20 m (50%) compared to shallower habitats (90%) in the Indian Ocean. Lower levels of light at deeper depths may contribute to lessening impacts, since combined effects of elevated levels of light and temperature together are more detrimental to corals than either one alone (Jokiel and Coles, 1990).

### Coral reproduction and dispersal

Reproductive activity (gametogenesis) in some important reef-building coral families (e.g. Pocilloporidae, Poritidae, and Agariciidae) in the Eastern Pacific can either be detrimentally affected or enhanced by ENSO-related seawater warming. Moderate to weak events can improve conditions for reproductive success since reproduction typically occurs under warmer conditions; however, strong events can cause reproductive failure if temperatures rise too high (Colley et al., 2006). Corals disperse to the tropical eastern Pacific via countercurrents that transport water from the west to the east. During ENSO warm phase, the intensity of these currents increase, possibly allowing a more rapid



transport of larvae and improved chances for dispersion and recruitment of corals originating in the Central Pacific to the Eastern Pacific (Glynn and Ault, 2000).

### Secondary biological impacts

Secondary impacts to corals following ENSO include bioerosion, predation, and increased susceptibility to disease. Accelerated rates of bioerosion by echinoids occur after coral skeletons are denuded of live tissue allowing overgrowth by algae. As the echinoids browse, they remove small amounts of carbonate, and when populations are high, entire reef structures can be eliminated. This was observed following the 1982–1983 ENSO, where pocilloporid reefs were reduced to sand and rubble by the echinoids *Eucidaris galapagensis* (in Galapagos) and *Diadema mexicanum* (in Panama) (Glynn, 1988; Eakin, 2001).

Reductions of coral populations directly affect their predators (corallivores), such as the Crown of Thorns starfish (*Acanthaster planci*). When less prey are available, predator populations decrease. Furthermore, focused predation on surviving coral colonies can result in addition loss of coral cover. Since ENSO-related mortality is greater in some coral species than others, prey switching may occur, especially if more desirable species suffer population declines (Glynn, 1990).

### Summary

El Niño, La Niña, and ENSO are related but distinct phenomena that affect corals, particularly in the eastern tropical Pacific. Teleconnections to adjacent regions also affect corals in the Western Caribbean, Central and Western Pacific, and the Indian Ocean. Elevated temperature anomalies result in up to 99% coral mortality in the most strongly affected areas. Other impacts related to ENSO, notably sub-aerial exposure associated with sea level decrease, also negatively affect corals.

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## Cross-references

Eastern Tropical Pacific Coral Reefs  
 Pacific Coral Reefs: An Introduction  
 Sea Level Change and Its Effect on Reef Growth  
 Sediments, Properties  
 Temperature Change: Bleaching  
 Upwelling and Coral Reefs  
 Waves and Wave-Driven Currents

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## ELECTRO MINERAL ACCRETION

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## Synonyms

Biorock; Electric artificial reef; Electro mineral accretion of minerals in seawater

## Definition

Electro mineral accretion (EMA) artificial reefs are metal structures used to secure transplants and promote the growth of scleractinian corals (Hilbertz and Goreau, 1996) and to provide a nature-like colonization substrate (Schuhmacher and Schillak, 1994).

EMA artificial reef structures act similar to an electrolytic cell. They consist of a metal frame upon which coral transplants are attached. An anode (made of a slowly oxidizing metal) is placed in the direct vicinity of the frame (cathode), with a weak DC electrical current applied to the set up. Sea water acts as the conductive electrolyte solution between the cathode and the anode. The applied electric current causes the deposition of minerals, such as  $\text{CaCO}_3$ ,  $\text{Mg}(\text{OH})_2$ ,  $\text{CaSO}_4$ , and  $\text{NaCl}$ , on the structure (Meyer and Schuhmacher, 1993; Hilbertz and Goreau, 1996). This is due to a reduction reaction taking place on the negatively charged cathode of the electrolytic cell (EMA artificial reef). The product of the reduction reaction which is of benefit to the corals is  $\text{CaCO}_3$ , as this is the primary compound that forms the skeletons of scleractinian corals.

The EMA process has been found to significantly increase growth rates of scleractinian coral transplants (Sabater and Yap, 2002, 2004; Eggeling, 2006). Increased skeletal growth rates have been attributed to an increase in mineral ion concentration within the vicinity of transplants attached to the cathode causing a diffusional influx of ions into the coral polyp's coelenterons, increasing the availability of ions for calcification (Sabater and Yap, 2004). Corals face a production trade-off between allocating resources into colony growth or production of reproductive cells (Rinkevich, 1996). Debate has developed regarding the use of habitat forming organisms with

artificially altered physiological traits in environmental restoration.

EMA artificial reefs have been installed for diving tourism (Van Treek and Schuhmacher, 1998) in many areas and have suffered from degrading natural coral reefs. They have also been promoted and implemented for coral reef restoration projects. Rapidly growing corals may have significant potential to be used in coral reef restoration projects for stabilizing substrate and promoting growth of key habitat forming species of coral. The technology has also been utilized for rapidly growing corals for use in aquaria (Eggeling, 2006).

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## Cross-references

Conservation and Marine Protection Areas  
 Reef Restoration

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## ELECTRON SPIN RESONANCE DATING (ESR)

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## Definition

The electron spin resonance (ESR) dating method is one of several radiation exposure methods based on radiation

dosimetry such as thermoluminescence (TL), optically stimulated luminescence (OSL), and radioluminescence (RL). All these methods use the phenomenon of common minerals acting as natural dosimeters. The radiation (natural radioactivity and cosmic rays) causes charge (electrons, free radicals) which is trapped at defects in the crystal lattice of a wide range of minerals such as aragonite, calcite, and quartz. Here, we will focus on dating aragonite coral samples. The trapped charges from paramagnetic centers can be detected by the rise of a characteristic ESR signal. The amount of trapped charge accumulation (paleodose,  $D_E$ ) increases with time and can be quantified by the ESR measurement. An ESR age is calculated by dividing the accumulated paleodose ( $D_E$ ) by the dose rate of the natural radiation ( $D'$ ) (Figure 1).

## Introduction

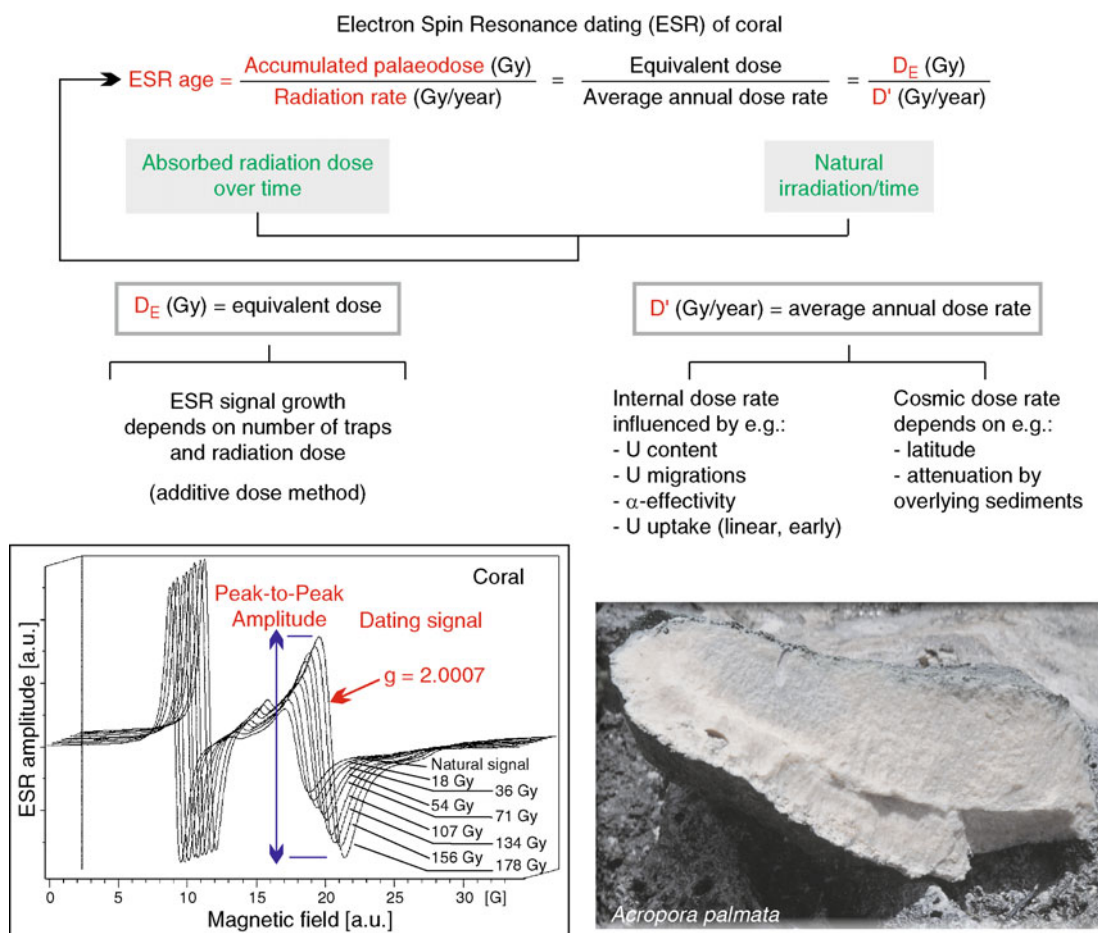
The first systematic studies and application of ESR dating of corals were published as early as the late 1980s (e.g., Ikeya and Ohmura, 1983; Radtke and Grün, 1988; Radtke et al., 1988; Grün et al., 1992), and since then several methodological improvements and the development of

more stable and high-resolution ESR spectrometers have significantly increased the quality of ESR dating results. Now, it is not only possible to distinguish between the major periods of high sea level during the last 500,000 years but also to differentiate between sub-maxima, for example, during the marine isotope stage (MIS) 5 sea-level highstand (e.g., Schellmann et al., 2004a; Schellmann and Radtke, 2004a). However, a precondition is that numerous corals from one stratigraphic unit and ideally from several locations are dated. Then, the effect of weak weathering and slight recrystallization from a primary aragonite to a calcite coral fabric and the resulting underestimation of the ESR ages can be detected from the scatter of individual results.

The high accuracy of ESR dating applied to corals is strongly supported by the comparison of ESR dating results with radiocarbon ( $^{14}\text{C}$ ) and thermal ionization mass spectrometry (TIMS)  $^{230}\text{Th}/^{234}\text{U}$  data.

## Methodology

Detailed overviews of the physics and the application of the ESR dating method have been provided, for example,



Electron Spin Resonance Dating (ESR), Figure 1. Generalized principle of ESR dating of aragonitic coral.



by Ikeya (1993), Grün (2007), Rink (1997), and Jonas (1997). Most recently, Schellmann et al. (2008) have reviewed the accuracy of ESR dating of different materials like coral, mollusc shells, and quartz; Blackwell (2006) has focused on ESR dating in Karst environments; and Grün (2006) has given a detailed description of ESR dating of human teeth.

As already stated, the ESR dating method uses the phenomenon that common minerals, like the aragonite fabric of corals, act as natural dosimeters. An ESR age is derived from the ratio of the accumulated radiation dose  $D_E$  (equivalent dose) to the natural radiation rate  $D'$  (dose rate), to which the sample was exposed in the past (Figure 1).  $D_E$  is determined by an additive dose method. For this method, 20 or more aliquots of the same sample are stepwise irradiated with increasing artificial  $\gamma$ -doses (e.g., using a  $^{60}\text{Co}$  gamma source). The growing amplitude of the ESR signal at  $g = 2.0007$  of a coral sample is proportional to the number of trapped charges ( $D_E$ ), which is dependent on the strength of natural irradiation (dose rate,  $D'$ ) and on the radiation time (= age of the sample). A living coral does not contain the ESR dating signal at  $g = 2.0007$ , which means that the ESR intensity is zero.  $D_E$  is determined by extrapolating the resulting dose response curve to zero ESR intensity. In the case of dating corals, the  $D_E$ - $D_{\max}$  plot procedure (D-DP procedure) should be used for the calculation of  $D_E$  as described by Schellmann and Radtke (2001). The former natural dose rate ( $D'$ ) of a coral sample is estimated on the basis of the content of uranium (other radioactive elements like Th and K are of no relevance) and the intensity of the cosmic dose rate. The correct determination of  $D'$  and  $D_E$  is essential for any ESR age estimation.

Improvements in annual dose rate ( $D'$ ) estimation and the newly developed approach of equivalent dose ( $D_E$ ) determination ( $D_E$ - $D_{\max}$  plot procedure) increase the precision of ESR dating of Holocene and Pleistocene corals (Schellmann et al., 2008). This is strongly supported by comparing ESR dating results with other numeric dating methods such as radiocarbon ( $^{14}\text{C}$ ) and TIMS U-series analysis (TIMS  $^{230}\text{Th}/^{234}\text{U}$ ).

### Case study 1: ESR dating of Pleistocene coral reef terraces

Since several early systematic studies have been carried out (e.g., Ikeya and Omuhra, 1983; Radtke and Grün, 1988), dating of corals is one of the most common applications of ESR dating. It has been widely applied for dating sequences of raised coral reef terraces with ages of up to 500–600 ka, e.g., on Sumba island (Pirazzoli et al., 1991); on Huon Peninsula, New Guinea (Grün et al., 1992); on Curaçao, Netherlands Antilles (Radtke et al., 2003; Schellmann et al., 2004b); and on Barbados (e.g., Radtke et al., 1988; Schellmann and Radtke, 2004a, b).

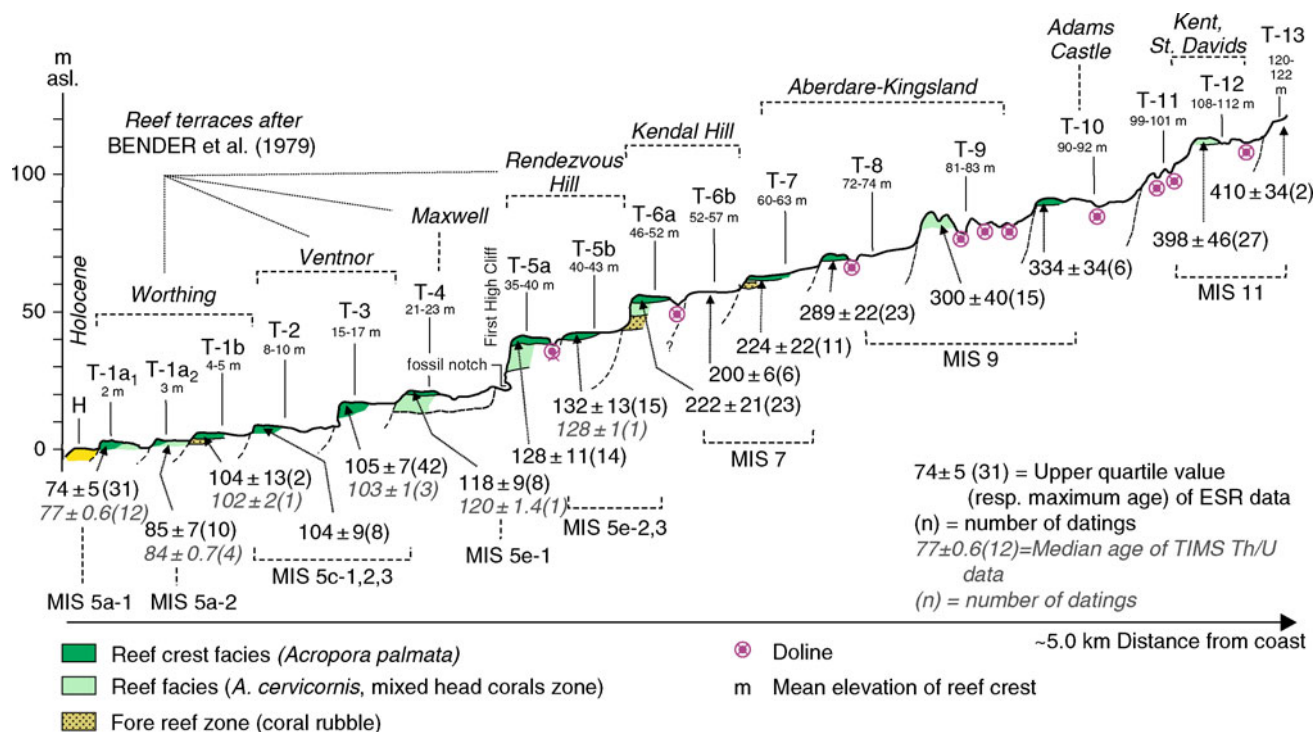
The ESR dating of the fossil coral reef terraces on Barbados provides an impressive example of the application of this method (e.g., Schellmann and Radtke, 2004a, b).

On this Caribbean island, several uplifted Pleistocene coral reef terraces are well preserved, rising up to 122 m above modern sea level in southern Barbados (Figure 2). By using morpho- and chronostratigraphic methods, the area between the present coastline and the center of southern Barbados can be subdivided up to 13 clearly distinguishable main coral reef terraces (T1 to T13) and some less prominent sub-levels (for example T-6a and T-6b, T-1a<sub>1</sub>, and T-1a<sub>2</sub>). The youngest formations are located at the lowest elevations close to the present coast, while older reef terraces have higher elevations and generally a greater distance from the coast. Due to the relatively slow uplift rate in southern Barbados (approx.  $0.27 \pm 0.02$  m/1,000 a), the youngest Pleistocene coral reefs (T-1a<sub>1</sub>) have been formed at approx. 74 ka (ESR) or 77 ka (TIMS Th/U) and the oldest and highest coral reef (T-13) during a sea-level highstand approx. 410 ka (MIS 11). This correlation between age and height of the terraces allows us to calculate neotectonic movements and to estimate paleo sea-level changes (e.g., Schellmann et al., 2004a; Radtke and Schellmann, 2005).

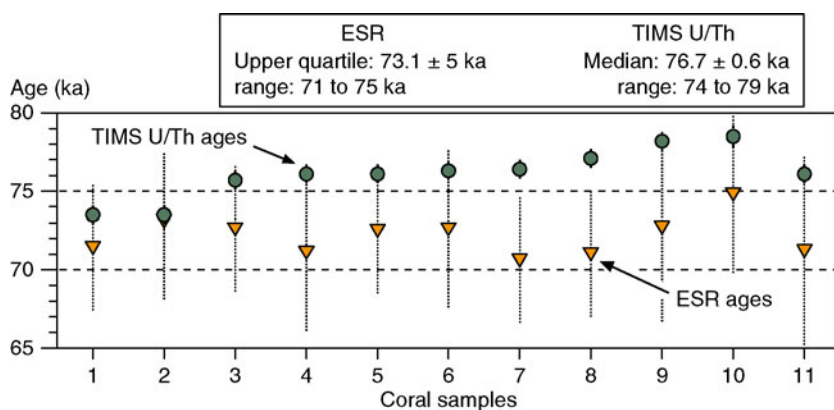
Generally, the timing of coral reef growth calculated by both dating methods agrees well, especially when the error ranges are considered. However, a detailed comparison of dating results of both methods shows that many ESR ages are up to 5–10% younger than the corresponding U-series ages, perhaps the result of a slight overestimation of the alpha-efficiency (0.05) used for ESR age calculations or of weak recrystallization processes that influence the ESR more strongly than the U-series data. The comparison also shows that the apparently minor analytical errors (precision) of U-series data (less than 1%, ESR between 5–8%) give no evidence of a better time resolution (Schellmann et al., 2004a). The latter can be demonstrated well by the relatively high scattering of both ESR and TIMS U-series data inside an individual Late Pleistocene coral reef deposit. For example, comparing the results of ESR and TIMS U-series dating of MIS 5a-1 corals, carried out on paired samples from Inch Marlowe Point location on Barbados (Figure 3), shows that the spread of individual ages (not considering errors) for both methods is about 4,000 years, although all ages were produced on individuals from the same branch of coral which are hence most likely of the same age (grown within not more than a few hundred years). Therefore, age differentiations between single Late Pleistocene coral reef deposits that have developed in time periods of less than 4,000–5,000 years are rarely reliable, independent of the applied dating technique (ESR or TIMS U-series).

### Case study 2: ESR dating of Holocene corals

The accuracy of ESR dating on paired samples of Holocene corals has been tested by Radtke et al. (2003) using 21 radiocarbon-dated Late and Middle Holocene coral samples from Tsunami deposits found on Bonaire and Curaçao (Netherlands Antilles) (Figure 4). The calibrated radiocarbon ages spread between recent and 3,644 years



**Electron Spin Resonance Dating (ESR), Figure 2.** ESR and TAMS U/Th ages of uplifted Pleistocene coral reef terraces from Southern Barbados. Details are provided in Schellmann and Radtke (2004a, 2004b).



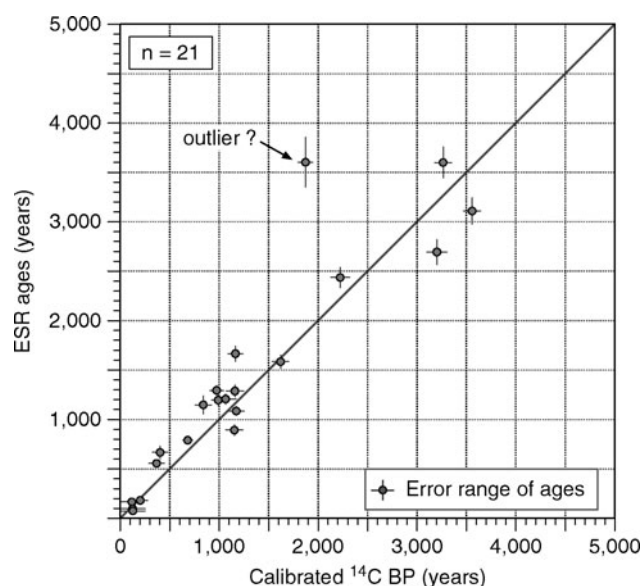
**Electron Spin Resonance Dating (ESR), Figure 3.** ESR and TAMS U/Th ages ( $\delta^{234}\text{U} > 141$  and  $< 157\text{‰}$ ) of MIS 5a-1 coral reef terrace near Inch Marlowe Point, southern coast of Barbados (slightly modified after Schellmann et al., 2004a).

and the ESR ages were between 9 and 3,653 years (not considering the individual uncertainties of each measurement). Except for one sample (outlier), the ages determined by both methods are consistent within an error range of approx. 250 years. Considering the small amplitude of the ESR dating signal from such young coral samples, the good agreement between radiocarbon and ESR data is astonishing. Nevertheless, U-series dating of

Holocene corals is much more precise than both ESR and radiocarbon dating.

### Summary

Due to methodological advances, which significantly increase the accuracy of ESR dating of Pleistocene and Holocene corals, ESR dating has become an efficient tool in earth sciences for geochronological studies on coral reef



**Electron Spin Resonance Dating (ESR), Figure 4.** Comparison of ESR and radiocarbon ages of Holocene corals from Aruba, Bonaire and Curacao (Netherlands Antilles). Calibrated radiocarbon ages were corrected for marine reservoir effect (slightly modified after Radtke et al., 2003).

terraces in the past decade. ESR dating of Holocene corals coincides with the variability of  $^{14}\text{C}$  ages caused by the marine reservoir effect, but without any doubt TIMS U-series dating of Holocene coral is more precise, much faster, and much cheaper than ESR dating. ESR dating of Pleistocene corals permits us to differentiate between the main marine isotope stages (MIS) 5, 7, 9, 11, and 13 as well as between the substages 5e-2,3 and 5e-1, 5c, and 5a-2 and 5a-1. The average error is about 5–8%. Late Pleistocene corals can be dated with a similar accuracy as with the TIMS U-series method in this time range, although the individual errors of ages are significantly larger than those of U-series data. The advantage of ESR, however, is that the upper dating limit for corals is probably above 500,000 years. If weathering and recrystallization from primary aragonite to calcite of the coral material could be excluded, dating of coral with an age of several million years should be feasible from the physical point of view. All in all, future research in ESR dating corals should be focused on (a) a more precise identification of diagenetic transformations of the primary aragonitic fabric of the coral samples and (b) on the creation of a single-aliquot dating technique that uses orientated aragonitic polycrystals.

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## Cross-references

Barbados  
 Electron Spin Resonance Dating (ESR)  
 Emerged Reefs  
 Last Interglacial and Reef Development  
 Sea Level Change and Its Effect on Reef Growth  
 Uranium Series Dating  
 Western Atlantic/Caribbean, Coral Reefs



## EMERGED REEFS

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### Synonyms

Coral terraces; Raised reefs; Reef terraces

### Definition

Emerged reefs are dead reefs (Figure 1), which emerge generally after the fall of the “relative” sea level due to various factors or triggers (1) uplifts in areas that are tectonically active; (2) the loading of the oceanic basins following the last deglacial sea-level rise (hydroisostatic readjustment); (3) decrease of the sea level resulting from glacioeustatic variations; and (4) lithospheric flexure. Consequently, the emerged reefs can be expressed by more or less narrow reef “flats” immediately at the rear of modern coral reefs, series of uplifted coral terraces, partly emerged coral buildups, and microatolls (see chapter *Microatoll*).

### Introduction

Emerged reefs are former living coral reefs, which are now subaerially exposed for several reasons. Emerged reefs have been observed in both the Caribbean and the Indo-Pacific. The presence of such emerged reefs was reported in the early works on coral reefs in various parts of the world. In 1842, Darwin reported the presence of raised coral reefs for example in Mauritius and in the Red Sea. He noted in 1842 that the “upraised coral islands in the Pacific” had not been examined by geologists. In 1872, Dana interpreted the presence of elevated reefs in the Pacific as resulting from uplift. Since these older works, several reasons have been invoked to explain the exposure

of these unique morphological features. Extensive series of emerged reefs can be observed in the tectonically active regions. One of the best studied series of coral terraces is located on the Huon Peninsula in Papua New Guinea (Chappell, 1974). This site provided vital information on the tectonic context and calculation of eustatic sea-level variations, made from the dating of corals from these terraces (Bloom et al., 1974; Chappell et al., 1996; Cutler et al., 2003). Other areas of tectonic uplift and reef terraces have also been studied as for example:

- In the Caribbean (Mesolella, 1967; Matthews, 1973; Bender et al., 1979; Blanchon and Eisenhauer, 2001; Feuillet et al., 2004), especially the well-known terraces from Barbados
- Vanuatu (Mitchell, 1968; Neef and Veeh, 1977; Taylor et al., 1980)
- Solomon islands (Mann et al., 1998; Taylor et al., 2005)
- Fiji (Nunn et al., 2002)
- Ryukyus (Konishi et al., 1974; Nakamori et al., 1995; Sagawa et al., 2001; Sasaki et al., 2004)
- Indonesia (Pirazzoli et al., 1991; Hantoro et al., 1994; Bard et al., 1995)
- Red Sea (Gvirtzman et al., 1992; El Moursi et al., 1994; Gvirtzman, 1994)

Lithospheric flexures are also one of the main causes invoked to explain the presence of raised atolls in certain parts of the Pacific as observed in the Cook-Austral islands (McNutt and Menard, 1978) or in New Caledonia (Dubois et al., 1974, 1988). Some recent emergence of corals and coral reefs can be attributed to isostatic readjustments as reviewed and analyzed in some Pacific islands by Grossman et al. (1998) and Dickinson (2001, 2004). Analyses of coral growth of microatolls also document minor vertical displacements (see Chapter *Microatoll*). In this chapter, the various types of “emerged reef” features will be reviewed and the main causes invoking the emersion of reefs and/or corals examined.

### Types of emerged morphological structures

The emerged reefs can be illustrated by several morphological features from series of coral terraces (Figure 2a and b) to slightly emerged reefs (Figure 3) to fields of single coral microatolls. However, emerged microatolls do not always relate to the type of emergence shown by other factors such as the removal of shingle ridges during storms which may result in a fall in low-tide water levels and leave former microatolls stranded.

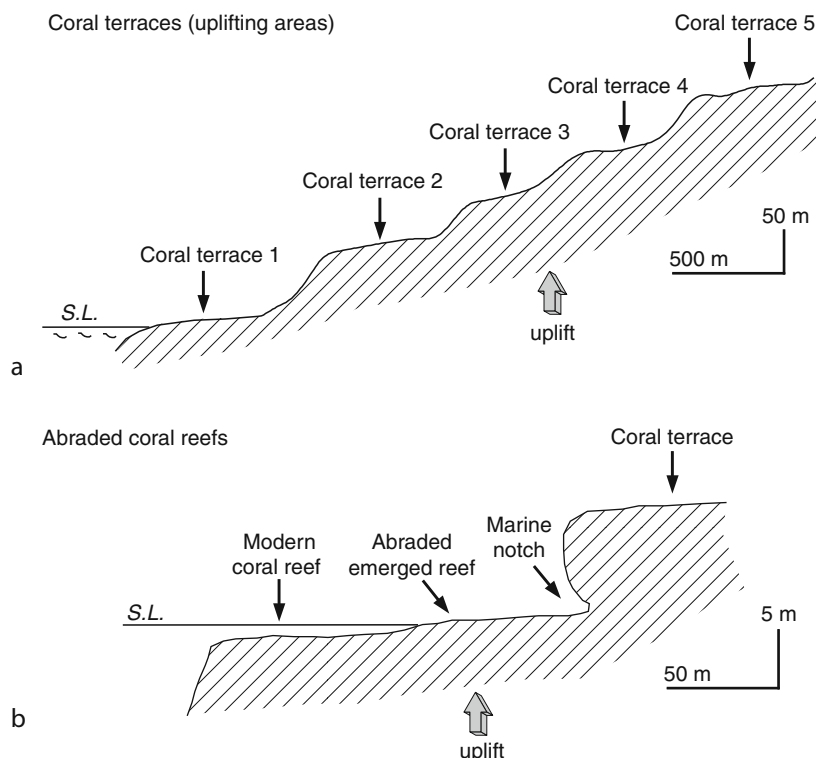
The major types of emerged reef structures are as follows.

#### Abraded reef flats

Emerged reefs can be found immediately behind the modern coral reef flats and very close to the modern sea surface (Figure 2b). Following an emersion (e.g., caused by a single tectonic event), the coral reef exposed to the waves, storms, and swell is rapidly abraded in a few years.



**Emerged Reefs, Figure 1** Emerged reefs in Vanuatu (photo G. Cabioch/IRD).



**Emerged Reefs, Figure 2** Various types of emerged reef features. (a) Coral terraces; (b) abraded reefs.



**Emerged Reefs, Figure 3** Remnants of slightly emerged reefs in Vanuatu (photo G. Cabioch/IRD).

Some of these abraded reef flats can be observed in the islands of insular arcs as for example in Vanuatu (Taylor et al., 1987).

### Coral terraces

Emerged coral reefs forming a series of terraces result over long periods of time from both glacioeustatic sea-level variation and from tectonic uplift (Figure 2a). These often

contain marine notches and are generally characterized by typical reef morphological features including reef crest, lagoon, etc. The most studied sequences are on Barbados (Mesoletta, 1967; Broecker et al., 1968) and on the Huon Peninsula in Papua New Guinea (Bloom et al., 1974; Chappell, 1974).

### Uplift in island arc archipelagos and tectonically active areas

The island arc archipelagos in tropical areas reveal the presence of elevated coral terraces. Coral dating coupled with morphological and paleoecological studies give information on both vertical motions and past sea-level variations over the Late Quaternary. Reconstruction of past sea levels can be made from calculations using the radiometric age of the emerged reef terraces and known rates of uplift [e.g., from the present elevation of the last interglacial (Stage MIS5e)]. Where rates of uplift are particularly high and relatively steady, terraces, which were originally below modern sea level (e.g., last glacial stadials and interstadials), have now emerged and allow the accurate calculation of these low sea levels.

Locations with intensive studies include Papua New Guinea (Bloom et al., 1974; Chappell, 1974; Chappell et al., 1996), Barbados (Broecker et al., 1968; Bender et al., 1979), Indonesia (Pirazzoli et al., 1991; Bard et al., 1995), Vanuatu (Neef and Veeh, 1977; Mitchell, 1968;

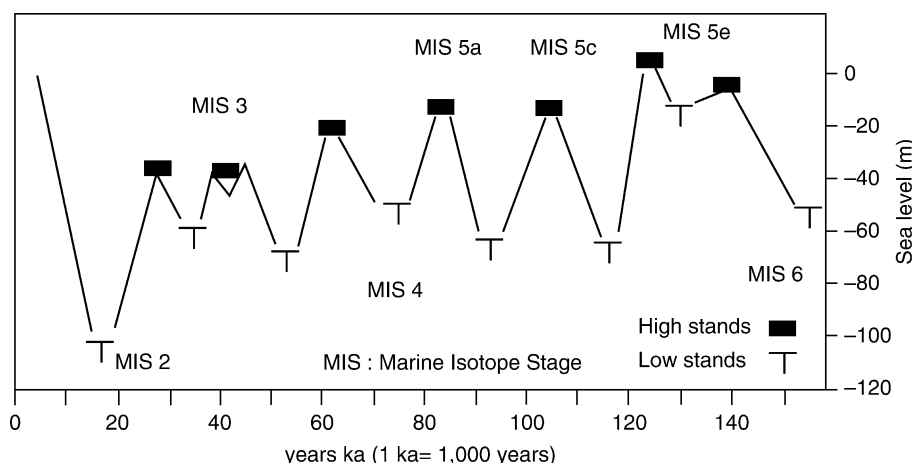
Jouannic et al., 1980; Taylor et al., 1980, 1987), and the Ryukyus (Konishi et al., 1974; Nakamori et al., 1995).

### Caribbean: Barbados

In the tectonically active region of the Caribbea (see *Barbados*), the Barbados emerged reefs are probably one of the most studied sequences of raised coral terraces and are, with the Huon Peninsula, one of the most important data set in the world on the knowledge of the Late Quaternary sea-level variations. Previous works by Mesolella (1967) showed the presence of up to 18 morphological emerged reef features and provided data on the ecology and the development of these formations. The lower terraces were dated by Uranium series dating giving ages of 122, 103, and 82 ka (1 ka = 1,000 years) (Broecker et al., 1968). These ages were found in the coral terraces and were labeled as Barbados I (+6 to +20 m depending on the sites and the uplift rate), Barbados II (+21 to +27 m), and Barbados III (+24 to +55 m), respectively. Taking into account the local uplift rate, Broecker et al. (1968) reconstructed the past sea-level variations of these periods. They obtained a 122-ka (corresponding to the Marine Isotope Stage 5e, MIS 5e) high stand at +6 m above the modern sea level and 103-ka (MIS 5c) and 82-ka (MIS 5a) high stands at -13 m below the modern sea level. These results were of broad importance, since they were (and still are) used as a world reference. Similar works were performed in several other sites on Barbados by Bender et al. (1979). Further studies on Barbados provided new data on the timing and the magnitude of these high stands (Schnellmann et al., 2004). Recently, a detailed survey on the distribution of reef facies performed in the west and south of Barbados provided a revised model of reef history during the last interglacial period (MIS 5) including three stages of development in relation to the sea-level variations (Blanchon and Eisenhauer, 2001).

### Pacific: Papua New Guinea

Chappell (1974) described in Papua New Guinea (PNG) (see *Huon Peninsula, P.N.G.*) a series of coral terraces on the Huon Peninsula, close to the New Britain trench at the boundary between the Australian and the Pacific tectonic plates. These terraces are characterized by a decrease of the uplift rate from south to north. They were first linked with sea-level variations by Fairbridge (1960, in Chappell, 1974). These terraces are represented by more than 20 elevated coral reefs, some of them revealing fossil reef crests and lagoons, and are particularly well developed along 80 km. They were dated by Veeh and Chappell (1970) at 30, 40, 50, 60, 80, 105, 120, 140, 185, and 220 ka, the higher by Uranium series dating. These authors underlined that the succession of such sea levels supports the Milankovitch astronomical theory, indeed, recording both eustatic sea-level variations and vertical motions (Chappell, 1974). In 1974, Bloom et al. reported new Uranium dates and proposed an improved sea-level variation curve for the last 125 ka (Figure 4). Among the flight of coral terraces, they identified the main "reef complexes" I, IIb, IV, V, VI, and VII dated at 5–9 ka, 41 ka, 61 ka, 85 ka, 107 ka, and 118–142 ka, respectively. Estimation of uplift rates was from the analyses of six cross sections and by comparison with the Barbados sea-level estimates. They proposed paleo-sea levels of +6 m, -15 m, and -13 m for the highstands of 125 ka, 103 ka, and 82 ka, respectively. The 60-ka, 42-ka, and 28-ka sea levels were estimated at -28 m, -38 m, and -41 m, respectively. Although numerous data were obtained in Papua New Guinea and in other sites including Barbados, some discrepancies appear between the sea-level record reconstructed from isotopic data (Marine Isotopic Stage, MIS) and coral dating (Chappell and Shackleton, 1986), especially the period ranging from 30 to 70 ka (=MIS 3). Chappell et al. (1996) "revisited" the sea-level estimates from PNG coral terraces taking into account new dates in the range of 30–62 ka and bathymetric range



**Emerg ed Reefs, Figure 4** Sea-level curve of the last 125 ka proposed by Bloom et al. (1974) (modified after Bloom et al., 1974).



of these dated corals. From these new results, there is a better constraint of the sea-level estimates between the isotopic data and the coral dating. New dates were obtained from the Huon Peninsula in 2003 by Cutler et al., using high-precision  $^{231}\text{Pa}$  and  $^{230}\text{Th}$  dating methods. They were focused on the Marine Isotope Stages 5 and 3. These authors provided data regarding the timing and the magnitude of the relative high stands and their transition during the MIS 5 sea-level variations. Moreover, some inputs were made on the relative sea-level variations of the MIS 3, with sea-level estimates ranging from 60.6 to 36.8 ka from between  $-85$  and  $-74$  m. In addition, all these studies on coral reefs from PNG provided information on deep ocean temperatures (Chappell and Shackleton, 1986; Chappell et al., 1996) highlighting the differences in the deep ocean temperature change from MIS 5 (125 ka) and MIS 2 (24 ka) and between Atlantic and Pacific Oceans (Cutler et al., 2003).

#### Pacific: Vanuatu

Vanuatu (see *Vanuatu*) is an island archipelago located in the South-West Pacific at the convergent boundary of the Australian, Pacific, and North Fiji Basin tectonic plates. Early works performed by Mitchell (1968) in Malakula, Neef and Veeh (1977) in Efáté, and Jouannic et al. (1980) and Taylor et al. (1980) in Espiritu Santo and Malakula revealed the presence of several elevated coral reefs. Even earlier, Stearns (1945) was one of the first scientists to try to interpret the presence of Pleistocene raised coral reefs in Espiritu Santo. In Efáté (or Vaté), Neef and Veeh (1977) identified sea levels of the last 125 ka by dating these emerged coral reefs. In the North of Malakula, previous works identified six main terraces culminating at about 350 m but some discrepancies in altitude occur, probably due to coral reworking and/or errors in altitude assignment (Mitchell, 1968; Jouannic et al., 1980). A survey performed in 2001 by Cabioch and Ayliffe provided more recent U/Th coral dating of these raised terraces and also observed several minor terraces. An estimate of the sea-level highstands from MIS 3 (55–40 ka) was given. These sea-level estimates are in good agreement with the data from PNG (Chappell et al., 1996). The North of the island of Malakula and the south and the east of the island of Espiritu Santo are also characterized by a series of raised terraces which were dated by Jouannic et al. (1980) and Taylor et al. (1980, 1987, 1990), providing information on vertical motions in relation to the D'Entrecasteaux Ridge collision (see Chapter *Vanuatu*). Moreover, in this area, Taylor et al. (2005) showed the occurrence of a Late Quaternary cycle of uplift and subsidence in Espiritu Santo over one or two hundred thousand years, interpreted as resulting from subduction of morphological features at the D'Entrecasteaux Zone.

#### Pacific: Solomon islands

South of Papua New Guinea and north of Vanuatu, the Solomon Islands, at the boundary convergence of the

Australian and Pacific tectonic plates, are also characterized by raised reefs. In comparison with studies performed in PNG and Vanuatu, very little is known about these raised terraces. Stearns (1945) indicated the presence of raised reefs in Guadalcanal, then in 1969, Stoddart extensively described the geomorphology of the Solomon Islands including elevated fringing and barrier reefs. Similarly to the Vanuatu archipelago, coral dating by Taylor et al. (2005) revealed the occurrence of a Late Quaternary cycle of uplift and subsidence in the central part of the New Georgia Island Group interpreted as resulting from subduction of the Coleman seamount or other prominent morphological features.

#### Pacific: Fiji

The islands of Fiji are located on the northern end of the Lau ridge, an old island arc. Elevated reefs were dated to the MIS 5 (125-ka highstand) (Nunn et al., 2002). Two alternative explanations were given by these authors to explain the elevation of these reefs. The Vanuabalavu island group could have been affected by the loading on the lithosphere inducing subsidence and reef uplift or alternatively it could be from the continuing anticlockwise rotation of the Fiji platform.

#### Pacific: Ryukyu

In the North-West Pacific, in the tectonically active region of the island arc at the boundary between the Amami Plateau in the Philippine Sea and the Eurasian tectonic plates, the Ryukyu Islands (see *Ryukyu Islands*) display sequences of emerged coral reefs. Kikai-Jima displays the highest uplift rate. These elevated reefs were described by several previous authors, and among these, Konishi (1974) provided Uranium and C14 dating of the five well-preserved coral terraces covering the period of the last interglacial period (the last 125 ka). Sugihara et al. (2003) focused their studies on the four Holocene raised coral reef terraces reaching an altitude up to 10 m and showed that these four terraces resulted from successive seismic uplifts. Sasaki et al. (2004), in the north of Kikai island, dated the coral terraces reaching an altitude from 15 to 65 m. The Uranium ages showed the occurrence of several reef sequences ranging from 75 to 51 ka. In addition to these works, older Pleistocene reef formations (400–500 ka) were described in the Ryukyus by Nakamori et al. (1995) based on geochronological dating and calcareous nannofossil biostratigraphy.

#### Indian Ocean: Indonesia

In Indonesia (see *Indonesian Reefs*), at the boundary of several tectonic plates, many islands display sequences of raised coral terraces. Chappell and Veeh (1978) in Atauro Island and in Timor reported some raised reefs reaching an altitude up to 600 m. In Atauro, the lowest terraces reaching a maximum of 65 m were dated as last interglacial (the last 125 ka). Later, additional sequences of raised reefs were described in the region of Sumba

Island (Pirazzoli et al., 1991; Bard et al., 1995) and again on Alor Island (Hantoro et al., 1994). In Cape Laundi (Sumba), Pirazzoli et al. (1991) described the occurrence of six reef complexes labeled I–VI, reaching an altitude of 475 m and dated by Electron Spin Resonance and Uranium series methods at 1 million years. The accurate dating of corals from the reef complexes I and II revealed a polycyclic origin for these terraces with ages from the MIS 5 (86, 105, 125 ka in the complex I and 130 ka in the complex II) and MIS 9 (280 and 355 ka in the complex II). The sequence of raised reefs on Alor Island described by Hantoro et al. (1994) is composed of six main coral terraces reaching an altitude of 700 m. Uranium series dating methods provided data to identify the terraces from the Holocene, MIS 5c, 5e, and 7. Based on the uplift rate of the dated terraces, an age was calculated for the highest terraces.

### Red Sea

The Red Sea (see *Red Sea and Gulf of Aqaba*) region is tectonically active as the Red Sea has been opened by sea-floor spreading. In this region, a series of raised terraces was reported by various authors. In the southern Sinai, Gvirtzman et al. (1992) reported the occurrence of several emerged reefs distributed into several morphological complexes. Gvirtzman (1994) performed a morphological description of these features and provided U/Th dating records for some of these terraces. Using these dates and taking into account the uplift rate, he estimated the age of other terraces which were not dated. As a result, ten low and high sea-level stands were identified from today to 330 ka. In another site in the Red Sea, in the coastal plain of Egypt, El Moursi et al. (1994) surveyed a sequence of eight emerged coral terraces including morphological description and Uranium series dating. The highest terraces labeled 8 reach an altitude ranging from 9 to 35 m, the intermediary terraces 5–7 from 22 to 32 m, and the lowest terraces 1–4 from 2 to 9 m. Because the coral from the highest terraces were recrystallized, only the lowest terraces 1–3 were dated from 72 to 131 ka with a large range of intermediary dates. These dates clearly indicate that these coral reefs were formed during the last interglacial period (125 ka, MIS 5). Based on the chronostratigraphy of the sea-level variations, these authors advanced the hypothesis that the terraces 5–7 were formed during the MIS 7 (230 ka) and the terrace 8 during the MIS 9 (330 ka).

### Lithospheric flexure

Emerged uplifted coral terraces and atolls can provide proof of the occurrence of lithospheric flexures due to a bulge at the rear of trenches or due to the loading of active volcanos in hotspot areas (e.g., Lambeck, 1981). In the central Pacific, McNutt and Menard (1978) observed the presence of raised atolls in the Cook and Society archipelagos in the vicinity of still or recently active volcanoes resulting from deformation caused by

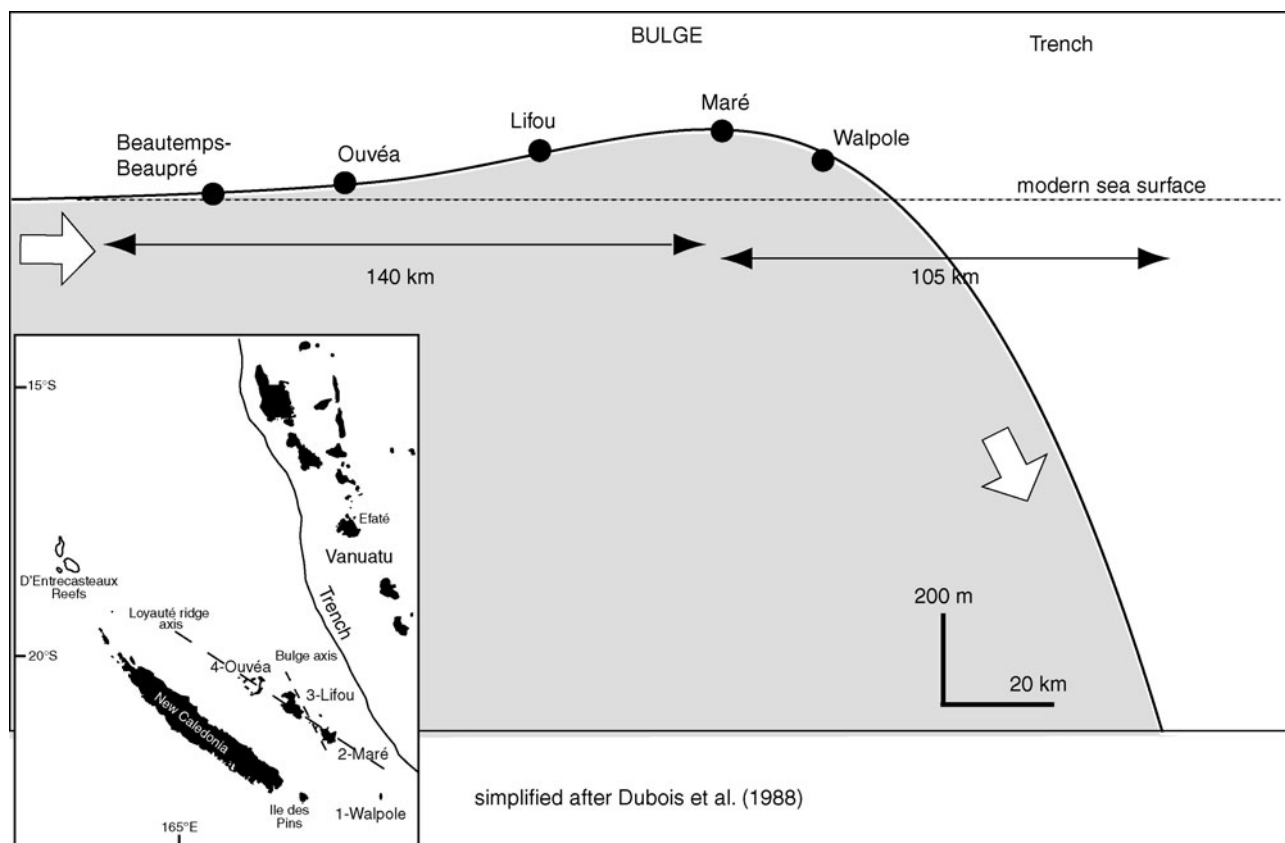
volcanic loading. They performed a model taking into account the elevation of these raised atolls which can give reliable data for the lithospheric flexure. Pirazzoli and Montaggioni (1998) dated some of the raised corals which were interpreted as resulting from this lithospheric flexure. The elevation of coral reefs in the vicinity of New Caledonia in the South-West Pacific provides another example of lithospheric deformation (Figure 5). The islands of the Loyalty ridge, from the south to the north, Maré, Lifou, and Ouvéa are uplifted close to the Vanuatu trench where the Australian plate dips beneath the Pacific plate and the North Fiji basin microplate. Only the eastern part of Ouvéa is uplifted, while the western part is still submerged. The uplift of the Loyalty Islands and the differences of elevation observed at Ouvéa illustrate particularly well the lithospheric deformation of the bulge formed just at the rear of the subduction zone (Dubois et al., 1974, 1988) as also confirmed by the magnetostratigraphy performed on Maré Island (Guyomard et al., 1996). Another example of lithospheric flexure marked by raised corals can be found in the Hawaii hotspot area (Grigg and Jones, 1997). Although the numerical models agree with the observations, these authors did not exclude the coexisting presence of tsunami deposits at this site.

### Isostatic readjustment

On numerous Indo-Pacific islands and reefs, less prominent emerged features have been described including abraded reef flats, emerged cemented deposits (beneath which in situ coral heads may occur), and microatolls growing at heights above that at which they grow today (e.g., Dickinson, 2004). A mid to late Holocene age has been established for these features, which generally show an emergence of between 1 and 3 m. The occurrence of this level and its altitude in 92 records from the Pacific were reviewed by Grossman et al. (1998). These islands far from the polar regions have been submitted to isostatic and gravitational readjustments resulting from the melt-water load on the oceanic floors and depending on the underlying mantle viscosity (Nakada, 1986; Nakada and Lambeck, 1989). Grossman et al. (1998) noted that the geophysical model of the rheological response to the last deglacial melting of the continental ice is in good agreement with the field data, i.e., 1–3 m higher than that present between 5 and 1.5 ka, (for example see Nakada and Lambeck, 1989; Lambeck and Nakada, 1990 for an Australian example). Variations occur even across continental shelves and between island groups and there is an absence of these features in the Caribbean where postglacial hydroisostatic emergence did not take place.

### Magma chamber inflation

In the volcanic island of Tanna (Vanuatu), some corals uplifted between 155 and 15 m were dated by Chen et al. (1995) of A.D. 1002 and A.D. 1878, respectively. The occurrence of such emerged corals at such an elevation was interpreted by the authors as resulting from the



**Emerged Reefs, Figure 5** Elevation on the lithospheric bulge of the uplifted reefs and atolls of the Loyauté Ridge (modified and simplified after Dubois et al., 1988).

magma chamber inflation of the active volcano Yasur. Moreover, they estimated the recurrence interval from 125 to 250 years.

### Summary

The emerged reefs can be expressed by several morphological features from the single coral colony (microatoll) to extensive development of coral terraces. Several causes can be invoked to explain the occurrence of emerged reefs in the various regions of the world. Among these causes, the uplift of coral reefs in tectonically active regions is probably the most widespread. Nevertheless, the occurrence of such coral terraces in these tectonic zones is also dependant on eustatic sea-level variations. Several sites in the world display extensive sequences of raised reefs including the well-known sites from Barbados in the Caribbean, Papua New Guinea and Vanuatu in the Pacific Ocean, and Indonesia in the Indian Ocean. Uplifted atolls in some parts of the world can also attest to the presence of lithospheric flexures as observed in the Cook-Society Islands or in the Loyalty Islands. Isostatic readjustments can be invoked to explain the mid-Holocene relative high sea level. The research carried out on these morphological features has highly improved

our knowledge of Late Quaternary climatic and eustatic sea-level variations, their tectonic context, and also the upper earth rheology. Further studies will provide additional data on these topics of broad interest in the framework of earth science.

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## Cross-references

Barbados  
 Density and Porosity: Influence on Reef Accretion Rates  
 Earthquakes and Emergence or Submergence of Coral Reefs  
 Glacial Control Hypothesis  
 Glacio-Hydro Isostasy  
 Huon Peninsula, P.N.G.  
 Indonesian Reefs  
 Last Glacial Interstadials  
 Last Glacial Lowstand and Shelf Exposure  
 Last Interglacial and Reef Development  
 Makatea  
 Megablocks  
 Microatoll  
 Mid Holocene  
 Pacific Coral Reefs: An Introduction  
 Radiocarbon ( $^{14}\text{C}$ ): Dating and Corals  
 Red Sea and Gulf of Aqaba  
 Ryukyu Islands  
 Sea Level Change and Its Effect on Reef Growth  
 Sea-level Indicators  
 Tsunami  
 Uranium Series Dating  
 Vanuatu  
 Volcanic Loading and Isostasy

## ENEWETAK ATOLL, MARSHALL ISLANDS

James E. Maragos

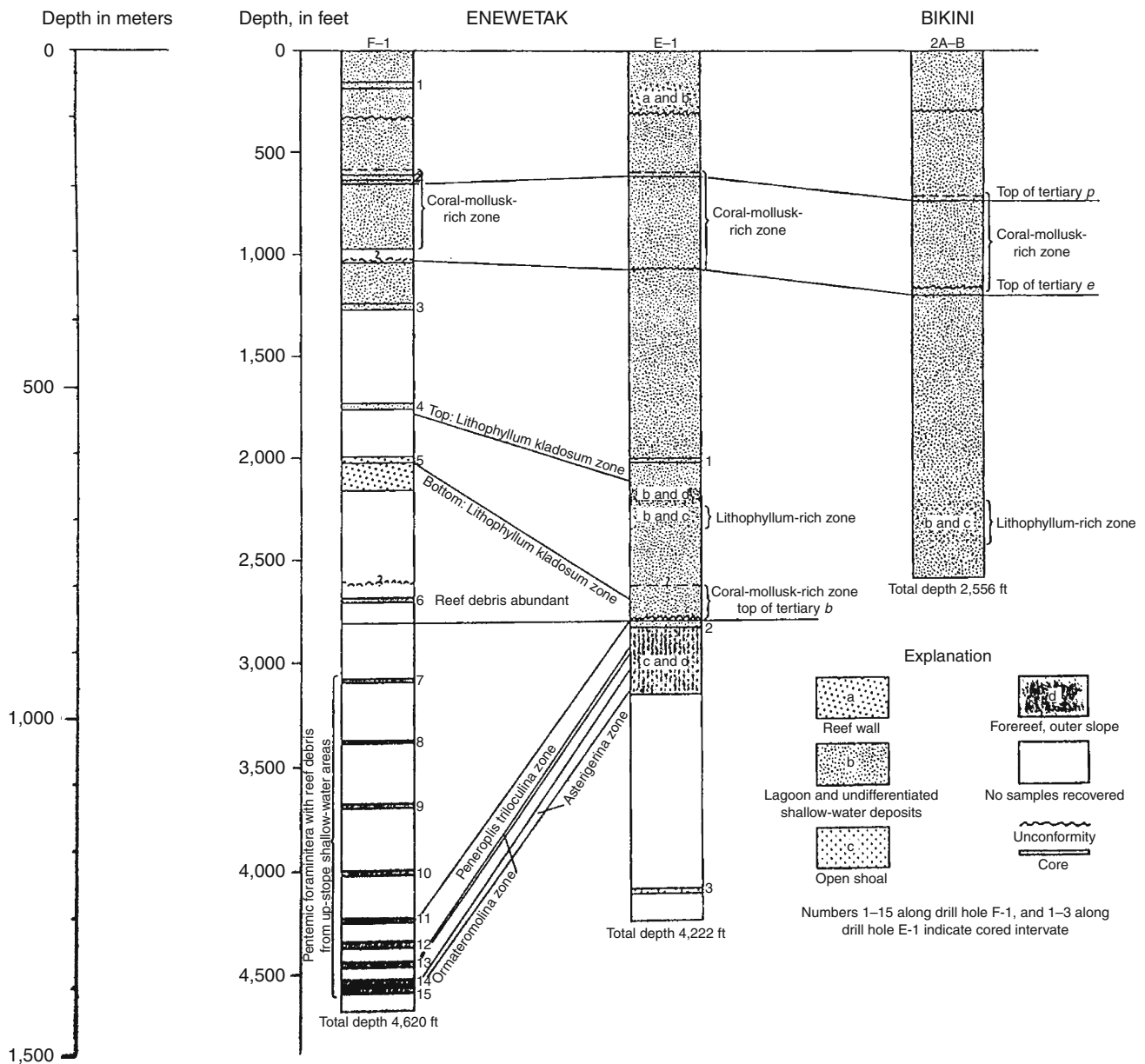
U.S. Fish and Wildlife Service, Honolulu, HI, USA

## Introduction

The Marshall Islands consist of 29 atolls and 5 isolated reef islands in the northwest central Pacific Ocean. The archipelago contains the largest and perhaps oldest atolls in the world based on the findings of deep drilling surveys at Enewetak (formerly called Eniwetok) and Bikini (Figure 1) and the archipelago's location near the oldest part of the Pacific Plate. Enewetak Atoll ( $11^{\circ}30'\text{N}$ ,  $162^{\circ}15'\text{E}$ ) (Figure 2) is located in the northwest corner of the Republic of the Marshall Islands, and is the second largest atoll in the Marshall Islands in terms of combined lagoon, reef, and land area ( $1,027\text{ km}^2$ ). Enewetak Atoll and neighboring Bikini Atoll collectively served as the major American proving ground for nuclear weapons testing after World War II that led to the most comprehensive scientific and engineering studies of deep ocean atolls in the world. Enewetak is part of the arid northern Marshall Islands where vegetation, groundwater, and rainfall ( $1,470\text{ mm/year}$ ) are less compared to those characterizing the central and southern Marshall Islands. However, rainfall can be highly variable ranging from 605 to  $2,422\text{ mm}$  per year. Surface ocean water temperatures normally range from  $25^{\circ}\text{C}$  to  $29^{\circ}\text{C}$  per year. The collective land area of the atoll is  $5.8\text{ km}^2$  with many larger islets concentrated on the eastern half and only smaller ones on the southwest quadrant of the atoll. The atoll supported 41 low coral islets mostly along the perimeter reef, until one on the northern rim (Elugelap) was first drilled and then completely destroyed and the other two (Sanil and Teiter) partially destroyed during the “Mike” hydrogen bomb test of 1952.

## Physical characteristics

The Enewetak perimeter reef shows a circumference of 122 km, and three large passes cut through the perimeter reef connecting the ocean to the lagoon. These occur along the southeast (1.5 km wide, 55 m depth), south (9.5 km wide, 10–20 m deep), and southwest (6 km wide, 2–4 m deep) parts of the perimeter reef. All show strong reversing currents during ebb and flood tides. The prevailing northeast trade winds generate wind waves that break on windward reefs and, via wave set-up, continually drive water across the perimeter reefs and into the northeastern lagoon regardless of the state of the tide. These cooler waters then sink toward the bottom of the lagoon, and warmer excess waters are eventually discharged through the three passes and over leeward SW reef crests. The large lagoon can be subdivided into four sectors depending on the degree of trade-wind fetch: the leeward lagoon in the northeast quadrant, the windward lagoon in the southwest quadrant, and the two transitional lagoon areas at the northwest and southeast quadrants.



**Enewetak Atoll, Marshall Islands, Figure 1** Comparative analysis of drill cores collected at Bikini and Enewetak Atolls, Marshall Islands (Schlanger, 1963 in Ristvet, 1987).

The windward perimeter reef shows distinct ecological and geological zones both at Enewetak and most of the remaining Marshall Islands (see “*Bikini Atoll, Marshall Islands*”). From offshore toward the lagoon, these zones include the following:

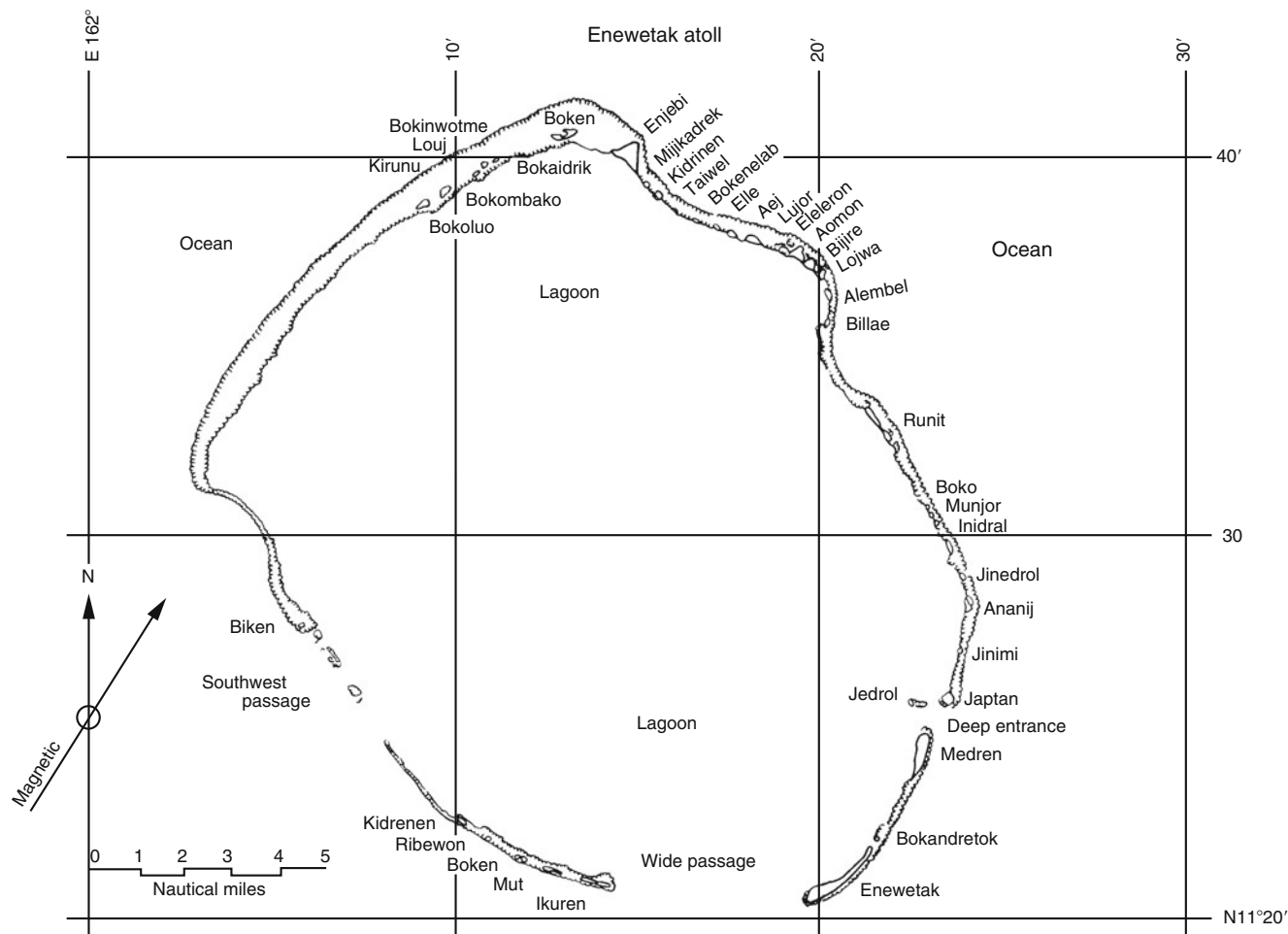
- Deep fore reef
- Fore reef terrace
- Spurs and grooves
- Coralline algal reef flat and ridge
- Room and pillar caverns (galleries)

- Micro-atolls (*Porites*, *Heliopora*)
- Moated reef flat
- Lagoon back reef and
- Lagoon floor

The windward reef flat also shows evidence of a higher (>1 m) sea-level stand between 2,200 and 4,000 years ago. The zonation along leeward (southwestern) perimeter reefs shows variable features including

- Shallow passes
- Sand flats





Enewetak Atoll, Marshall Islands, Figure 2 Map of Enewetak Atoll with the Marshallese names of the islands (Reese, 1987).

- Pinnacles
- Coralline algae reef flat with emergent corals (*Acropora*, *Pocillopora*)
- Massive buttresses
- Canyons
- Amphitheatres and
- Steep leeward fore reef slopes

Approximately 158 patch reefs reach the sea surface in the lagoon, and an estimated 3,000 pinnacle reefs, each with at least 4 m of vertical relief, are in the subsurface lagoon that has a maximum depth of 65 m.

### Cultural history

Based upon Marshallese oral tradition, archaeology, and linguistics, the Marshall Islands (including [Enewetak Atoll, Marshall Islands](#)) may have been inhabited for as long as 2,000–3,000 years with the initial explorers beginning their migrations from the Philippine region of South-east Asia approximately 5,000 years ago. The Marshallese

are bonded by a singular culture and language, and the archipelago is divided into two northwest-to-southeast trending geological and cultural chains termed the Ralik (“sunrise”) and Ratak (“sunset”), each with separate leadership hierarchies and cultural lineages. All of the remaining islands and atolls in the archipelago are inhabited except for six arid northern atolls (Ailinginae, Bokaak, Bikar, Taka, Erikub, and Rongerik), one small southern atoll (Ngarikrik), and one central isolated reef island (Jemo). These eight likely served as pantry reserves for neighboring inhabited atolls. The remaining atolls and reef islands were all likely continuously settled except during temporary evacuations from natural disasters. However, from 1946 to 1954 the peoples of Utirik, Rongelap, Enewetak, and Bikini were forced to evacuate their home atolls during the U.S. nuclear testing program, and all have been, or are being resettled, except for Bikini (see “[Bikini Atoll, Marshall Islands](#)”).

The people of Enewetak are the original and only inhabitants of Enewetak Atoll, according to their oral

tradition that also maintains they have lived at their home atoll since the “beginning of time.” The two largest islands, Enewetak in the SE and Engebi in the NE, have served as the two main villages at the atoll. Because of their geographically isolated locale, the Enewetak people and culture as a whole have evolved separately in some respects from their neighbors at the remaining Marshall Islands. Before the previous century, the Enewetak people were known for their long distance travel and navigation, visiting the inhabited islands of the Caroline archipelago to the southeast. They were also known as builders of the largest ocean-going canoes (15 m in length) constructed in the Marshalls at that time.

### Recent history

The Spanish explorer Alvaro de Saavedra is credited for the European discovery of Enewetak Atoll in 1529. Afterward, Enewetak was visited only once in 1792 before Captain Fearn of the vessel *Hunter* mapped the atoll in 1794. In 1898, Germany declared the Marshalls and several other Pacific areas as Protectorates, and a German trader contracted the Enewetak people to extend their plantings to promote the copra trade at Enewetak Atoll and another atoll, Ujelang. Before this time, the Enewetak people never relied much on Ujelang, a much smaller atoll 200 km to the southwest. Ujelang was previously inhabited by a separate clan of Marshallese until most were wiped out by a typhoon near the end of the nineteenth century, with the survivors later migrating to the southern Marshall Islands and never returning.

Japan took possession of most German territories in 1914 when World War I began, including the Marshall Islands and retained custody of them after the war and defeat of Germany via a Mandate from the League of Nations. For 30 years, Japan administered Enewetak from its headquarters at Pohnpei Island in the Caroline Islands because of its closer proximity vis-à-vis the Jaluit Atoll headquarters in the southern Marshalls. In turn, this further isolated the Enewetak people from the remaining Marshallese during the next 3 decades. Japanese rule initially focused on trade, but after 1935, and in violation of the Mandate, Japan began construction of military bases and airstrips throughout the Marshalls, including at Engebi and Enewetak Islands on Enewetak Atoll. The Enewetak islanders were caught in the crossfire during the January 1944 battle of Enewetak between Japanese and American forces. A tenth of the islanders were killed, and virtually all their food crops, vegetation, and dwellings at Enewetak and Engebi Islands were destroyed by the heavy initial bombardment. After the battle, the Americans moved the Enewetak survivors to two small eastern islets at the atoll. By early 1946, the Americans had built a military base at Enewetak and convinced the 141 islanders to temporarily resettle at Ujelang Atoll in order to make way for the nuclear testing program. The islanders did not return to their home atoll for 34 years,

after numerous false promises and 43 nuclear tests from 1948 to 1958 (Table 1, Figure 3) at Enewetak.

### The Nuclear Era

The Americans soon included both Bikini and Enewetak as part of a new U.S. Pacific Proving Ground. The Enewetak islanders remained at Ujelang despite dwindling subsistence resources, expanding population, substandard living conditions, and infrequent visits by supply vessels at the much smaller atoll. Meanwhile at Enewetak, the force of some of the nuclear tests was underestimated, others malfunctioned, and some islands became heavily contaminated with radionuclides, and remained unsafe for resettlement and agricultural use unless cleaned up. In particular, the “Mike” test of 1952 was the first atmospheric detonation of a hydrogen bomb, and created a large crater nearly 2 km across, resulting in the fracturing and slumping of a portion of the northern fore reef just north of the crater (Figure 4).

Finally in 1972, after the threat of protest and legal action, the United States agreed to resettlement after “unspecified activities” were completed. These activities were later determined to be the Pacific Area Cratering Experiments (PACE) designed to evaluate the geological characteristics of cratering from some past nuclear tests by examining existing bomb craters and also simulating their effects by detonating large quantities of conventional explosives at targeted reefs. The PACE program refrained from using radio-nuclides to insure compliance with the provisions of the Partial Test Ban Treaty ratified in 1963. After learning about the potential physical damage from the PACE proposal at a community meeting, the Enewetak people labeled PACE as “evil” and directed their attorneys to sue in U.S. Federal Court, demanding that the proposal be subject to the U.S. Environmental Policy Act. Subsequently, the United States dropped the PACE project, and in 1976 agreed to finance a partial resettlement.

Of particular concern was the incomplete combustion of one test conducted at Runit Island leading to the scattering of plutonium 239 over the island and reef. Given the half life of the isotope is now estimated at 24,000 years (Argonne National Laboratory, 2005), this posed a serious threat to the returning islanders. The United States budgeted \$120 million to collect and place contaminated soil mixed with concrete into Cactus Crater north of the island, and cap it with an 18-in. thick concrete dome (Figure 5a and b). Nevertheless, there was more contaminated soil at Runit than could be encrypted, and a further decision was made to ban the island from all visitation and use indefinitely. After the United States completed other cleanup actions, the remaining 543 Enewetak people were finally repatriated to their home atoll in 1980. Since then the population has fluctuated between 800 and 1,000 residents. In 2000, the Marshall Islands Nuclear Claims Tribunal awarded more than \$340 million to the Enewetak people for loss of use, hardship, medical difficulties, and further nuclear cleanup.

**Enewetak Atoll, Marshall Islands, Table 1** Nuclear tests at Enewetak Atoll, 1948–1958. (After Helfrich and Ray, 1987)

| Event name              | Date     | Type and Height (ft) | Yield             | Code location       | Island    |
|-------------------------|----------|----------------------|-------------------|---------------------|-----------|
| Sandstone               |          |                      |                   |                     |           |
| X-ray                   | 4-14-48  | Tower 200            | 37 KT             | Janet, W tip        | Engebi    |
| Yoke                    | 4-30-48  | Tower 200            | 49 KT             | Sally               | Aomon     |
| Zebra                   | 5-14-48  | Tower 200            | 18 KT             | Yvonne, N tip       | Runit     |
| Greenhouse              |          |                      |                   |                     |           |
| Dog                     | 4-7-51   | Tower 300            | Yvonne, N end     | Runit               |           |
| Easy                    | 4-20-51  | Tower 300            | 47 KT             | Janet, W tip        | Engebi    |
| George                  | 5-8-51   | Tower 200            | Ruby              | Eleleron            |           |
| Item                    | 5-24-51  | Tower 200            | Janet, N tip      | Engebi              |           |
| Ivy                     |          |                      |                   |                     |           |
| Mike                    | 10-31-52 | Surface              | 10.4 MT           | Flora               | Elugelap* |
| King                    | 11-15-52 | Airdrop 1500         | 500 KT            | Yvonne 2000' N      | Runit     |
| Castle                  |          |                      |                   |                     |           |
| Nectar                  | 5-13-54  | Barge                | 1.69 MT           | Mike Crater         | *         |
| Redwing                 |          |                      |                   |                     |           |
| Lacrosse                | 5-4-56   | Surface              | 40 KT             | Yvonne, N end       | Runit     |
| Yuma                    | 5-27-56  | Tower 200            | Sally, W tip      | Aomon               |           |
| Erie                    | 5-30-56  | Tower 300            | Yvonne airstrip   | Runit               |           |
| Seminole                | 6-6-56   | Surface              | 13.7 KT           | Irene               | Boken     |
| Blackfoot               | 6-11-56  | Tower 200            | Yvonne, middle    | Runit               |           |
| Kickapoo                | 6-13-56  | Tower 300            | Sally, N tip      | Aomon               |           |
| Osage                   | 6-15-56  | Airdrop 670          | Yvonne, middle    | Runit               |           |
| Inca                    | 6-21-56  | Tower 200            | Pearl             | Lujor               |           |
| Mohawk                  | 7-2-56   | Tower 300            | Ruby              | Eleleron            |           |
| Apache                  | 7-8-56   | Barge                | Mike Crater       | *                   |           |
| Huron                   | 7-21-56  | Barge                | Mike Crater       | *                   |           |
| Hardtack, Phase I       |          |                      |                   |                     |           |
| Cactus                  | 5-5-58   | Surface              | 18 KT             | Yvonne, N end       | Runit     |
| Butternut               | 5-11-58  | Barge                | Yvonne, 4000' SW  | Runit               |           |
| Koa                     | 5-12-58  | Surface              | 1.37 MT           | Gene                | Teiter    |
| Wahoo                   | 5-16-58  | Underwater 500       | James, 7400' S    | Ribewon             |           |
| Holly                   | 5-20-58  | Barge                | Yvonne, 2075' SW  | Runit               |           |
| Yellowwood              | 5-26-58  | Barge                | Janet, 6000' SW   | Engebi              |           |
| Magnolia                | 5-26-58  | Barge                | Yvonne,           | 3000' SW            | Runit     |
| Tobacco                 | 5-30-08  | Barge                | Janet, 4000' SW   | Engebi              |           |
| Rose                    | 6-2-58   | Barge                | Yvonne, 4000' SW  | Engebi              |           |
| Umbrella                | 6-8-58   | Underwater 150       | Glenn, 7400' N    | Ikuren              |           |
| Walnut                  | 6-14-58  | Barge                | Janet, 6000' SW   | Engebi              |           |
| Linden                  | 6-18-58  | Barge                | Yvonne, 2000' SW  | Runit               |           |
| Elder                   | 6-27-58  | Barge                | Janet, 4000' SW   | Engebi              |           |
| Oak                     | 6-28-58  | Barge                | 8.9 MT            | Alice reef, 3 mi SW | Bokoluo   |
| Sequoia                 | 7-1-58   | Barge                | Yvonne, 2000' SW  | Runit               |           |
| Dogwood                 | 7-5-58   | Barge                | Janet, 4000' SW   | Engebi              |           |
| Scaevola                | 7-14-58  | Barge                | Yvonne, 561' SW   | Runit               |           |
| Pisonia                 | 7-17-58  | Barge                | Yvonne, 12,000' W | Runit               |           |
| Olive                   | 7-22-58  | Barge                | Janet, 4000' SW   | Engebi              |           |
| Pine                    | 7-26-58  | Barge                | Janet, 8500' SW   | Engebi              |           |
| Quince                  | 8-6-58   | Surface              | Yvonne, middle    | Runit               |           |
| Fig                     | 8-18-58  | Surface              | Yvonne, middle    | Runit               |           |
| <b>TOTALS: 43 tests</b> |          |                      |                   |                     |           |

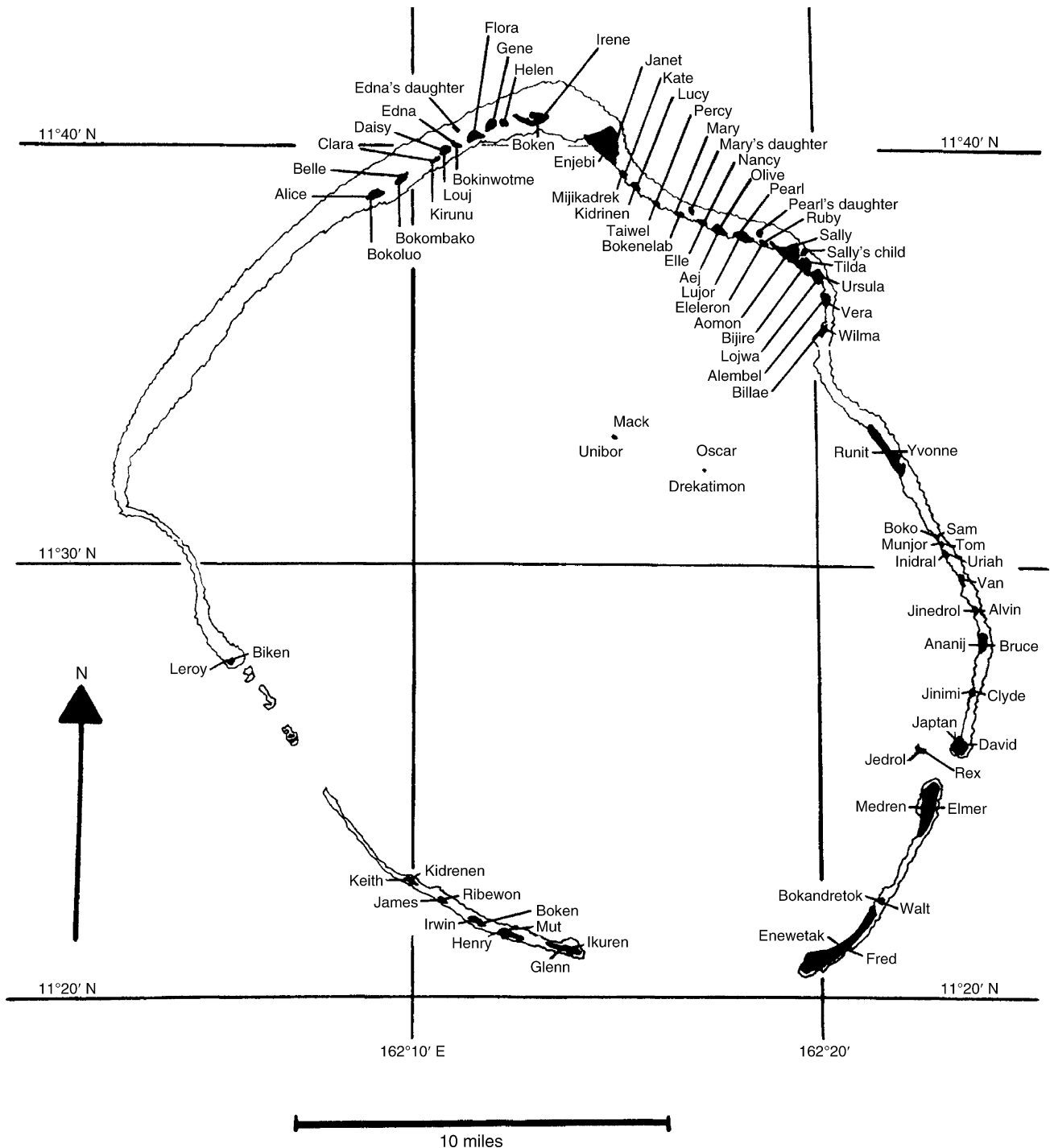
Asterisk (\*) = Elugelap Island destroyed and site became Mike Crater after 10-31-52.

### Enewetak Marine Biological Laboratory

After the initial operations crossroads nuclear tests at Bikini Atoll were completed in 1946, considerable civilian-based research on the geology, oceanography, and ecology of atoll ecosystems was encouraged alongside military-applied research focusing on the impact of the nuclear weapons and movement of radioactivity within

food webs of the atoll and marine ecosystems. Much of this was funded by the Office of Naval Research and the fledgling Atomic Energy Commission (AEC). A Pacific Science Board of the National Academies of Science was established, and many top scientists and engineers were engaged in research including those at the U.S. Geological Survey, Lawrence Livermore National Laboratory,



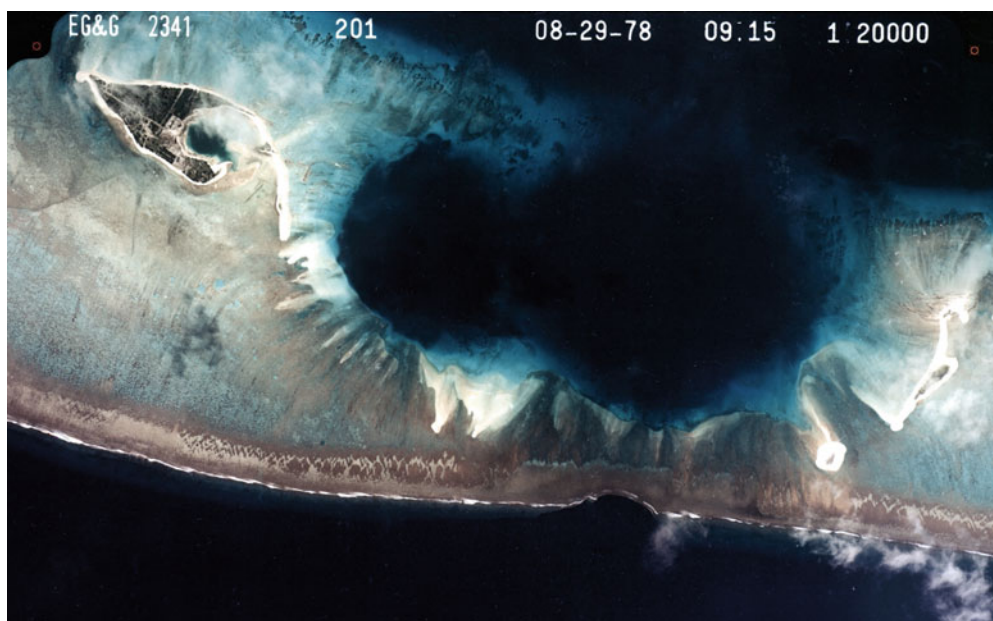


**Enewetak Atoll, Marshall Islands, Figure 3** Islands of Enewetak Atoll with Marshallese names shown on the lagoon side and the English U.S. government code names on the ocean side (Helfrich and Ray, 1987).

Brookhaven National Laboratory, and dozens of other leading research institutions. A periodical "Atoll Research Bulletin" was initiated in 1950 for publishing new scientific findings on atolls, and the *U.S. Geological*

*Professional Paper* series was expanded to accommodate the results of extensive geological research.

In 1954, Dixie Lee Ray, Director of the Atomic Energy Commission, provided funding for a marine biological



**Enewetak Atoll, Marshall Islands, Figure 4** An aerial view of the large Mike and adjoining Koa bomb craters at the northern rim of Enewetak Atoll in 1978. Note the indentation in the northern ocean-facing reef showing where the Mike hydrogen bomb test caused the spalling and collapse of a sliver of the reef. (Photo courtesy by EG&G Electronics in Tipton and Meibaum, 1981).

laboratory to be established at Enewetak to promote the opportunity for other scientists to visit and engage in field research at the atoll. The Enewetak Marine Biological Laboratory was established in 1955 and directed by marine scientists at the University of Hawaii. Still later the laboratory was reorganized and renamed the Mid-Pacific Marine Laboratory in 1975 to add neighboring Bikini Atoll to the research focus. In 1979, with the cleanup of Enewetak nearing completion, the laboratory was renamed the Mid-Pacific Research Laboratory and down-phased to concentrate on synthesizing the research of the previous quarter century and promoting terrestrial research.

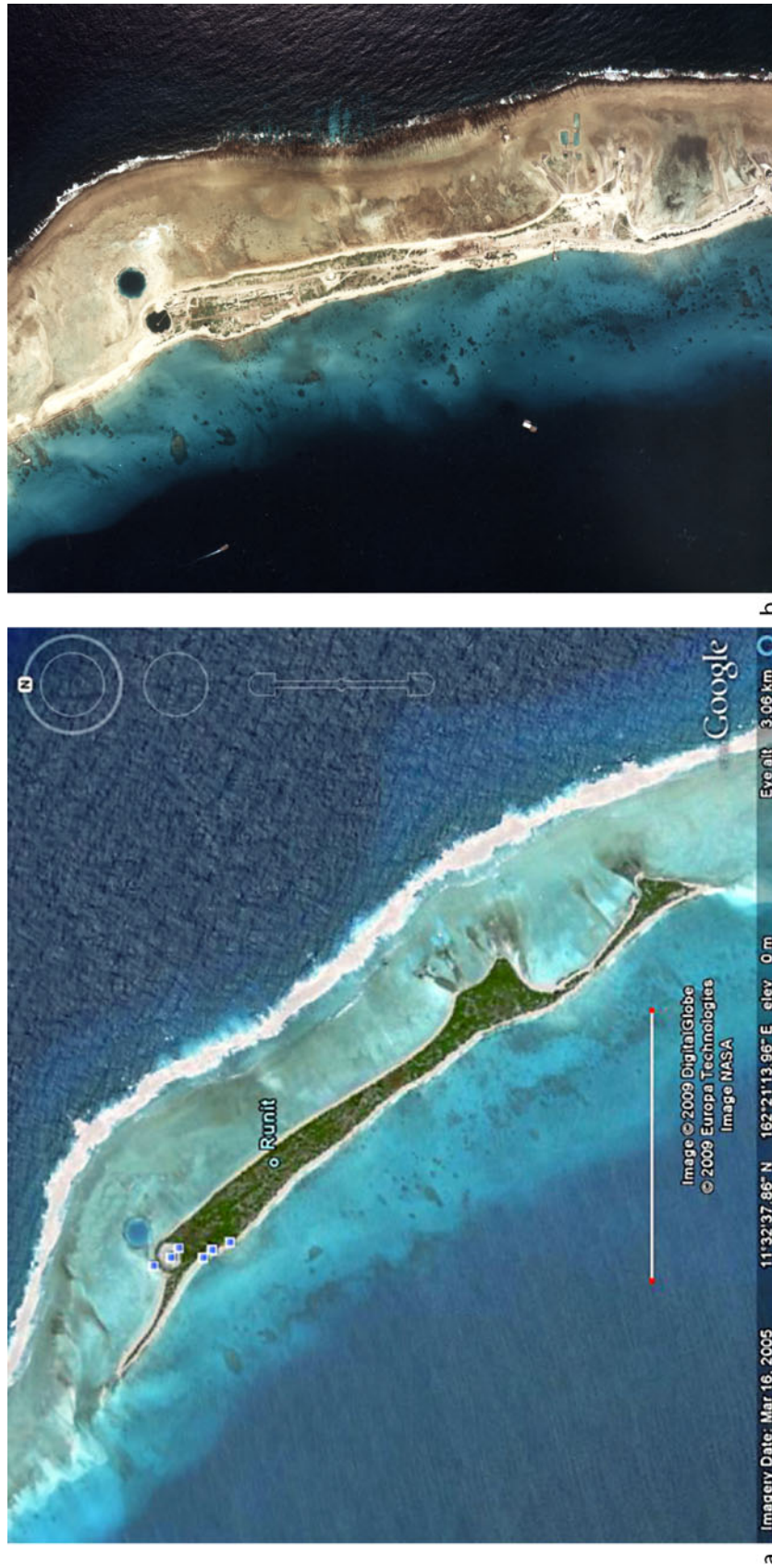
With the resettlement of the Enewetak people completed in 1980 and the subsequent reduction in AEC budgets, the laboratory was closed in 1985 with its biological collections packed and transferred to the Bernice P. Bishop Museum and the Smithsonian's National Museum of Natural History. The reference library of the lab was transferred to the Hawaii Institute of Marine Biology of the University of Hawaii in Kāne'ohe Bay. Over the 30-year period of the lab, 250 formal publications were produced, more than a thousand contributions accessioned, and 1,028 scientists utilized the laboratory. A two volume synthesis of marine research at the lab, *The Natural History of Enewetak Atoll*, was prepared by three dozen scientists and published by the U.S. Department of Energy in 1987.

### Deep Drilling Program at Enewetak Atoll

The earliest modern drilling to learn of the origin of atolls began at Funafuti when British scientists in 1896

penetrated 114 ft. Additional efforts by Japanese scientists led to the drilling at North Borodino to a depth of 1,416 ft. American scientists drilled six holes at Bikini in 1947, two of which penetrated to 1,346 and 2,556 ft. Although all cores had provided evidence of carbonate deposits forming in shallow waters, including corals that had grown in place, none penetrated far enough to reach volcanic base of the atolls. However, in 1951, one Enewetak drill hole at Medren Island off the southern rim penetrated to 4,222 ft (1,267 m) and another Enewetak drill hole at Elugelab Island along the north rim reached to 4,610 ft (1,405 m), with both hitting volcanic bedrock of the upper slope of an extinct volcano rising 5,000 m above the surrounding deep ocean floor, and serving as the base of the atoll. The reef cap above the volcano was estimated at 1,370 m in vertical thickness, and the basalt at the bottom of the cores was dated from the Eocene at 51–59 million years before present. These drillings provided the necessary evidence in support of Darwin's subsidence theory leading to deep ocean atoll development. All material collected in the two deep Enewetak cores was limestone with numerous cavities, characteristic of shallow living reefs, and dominated by corals, coralline algae, mollusks, and foraminifera that grew and survived only in shallow water.

Since these species cannot survive below 50–100 m, they must have lived and calcified when they were in shallow waters, meaning that the volcanic foundations had experienced subsidence. Olivine basalts as well as those dredged up offshore on the deep slopes of Enewetak Atoll provide the physical proof that ancient oceanic volcanoes are the bases of atolls in the central Pacific. Additional tuff



**Enewetak Atoll, Marshall Islands, Figure 5** Aerial image of Runit Island and the Cactus and LaCrosse craters during and after the cleanup in 1978 and 2005 respectively: (a) Runit Island in 1978 along the northeastern rim of Enewetak Atoll and the two craters at the north end of the island during cleanup involving removal of contaminated soil and placement in Cactus crater (EG&G Electronics in Tipton and Meibaum 1981). (b) Runit Island in 2005 photo showing recovery of vegetation and the two craters at the northwest end of the island: Cactus, with the concrete dome (on the island) and LaCrosse (to north on ocean facing reef flat). A total of 17 of the 43 total nuclear tests at Enewetak were conducted on or within 2 miles of Runit Island (Google Earth, DigitalGlobe, Europa Technologies, and the National Aeronautical and Space Administration, 2009).



and volcanic glass deposits added further evidence that the volcano erupted at sea level after the Paleozoic, leading to the conclusion that the volcano reached sea level early in its growth and then later subsided to serve as the base for future reef growth, leading to the contemporary atoll of Enewetak. Numerous additional drillings were made at the atoll during the latter PACE program to reinforce and add to the earlier findings.

It is possible that coral settlement and fringing reef growth may have begun soon after basalt islands emerged in the Cretaceous or Eocene, lengthening the time when corals and other reef builders first established at an earlier age, and lengthening the process of biological evolution thereafter. The fossil corals retrieved and identified by John Wells from the Enewetak cores revealed 15 species and 3 genera that no longer exist. These species may have gone extinct or evolved into different species over time. Likewise, 21 species of fossil foraminifera and 3 fossil

species of sea urchins are also reported from the cores. In essence, the growth of the atoll reef over geological time has transcended the evolution of the reef builders that participated in its early construction.

### Biogeography and ecology

Extensive marine biological surveys were accomplished between 1947 and 1986 including dredge hauls, free diving, and hookah collections during the first decade and transitioning to scuba diving, remote operated vehicle surveys, and submersible dives during later surveys. More than 4,600 species of marine life have been collected and described from Enewetak (Table 2). These include more than 180 species of stony corals and more than 800 species of near shore fishes reported at Enewetak Atoll. Although the coral totals are higher than those reported at the smaller atolls at the north end of the archipelago, they are substantially lower than the 268 species of corals now reported at

**Enewetak Atoll, Marshall Islands, Table 2** Diversity levels of biota categories inventoried at Enewetak Atoll to 1987 (Compiled by Burch in Devaney et al., 1987)

| Taxa                                | # Species | # Genera | # Families | Sources in Devaney et al. (1987) |
|-------------------------------------|-----------|----------|------------|----------------------------------|
| Algae                               | 238       | 106      | 40         | Tsuda                            |
| Fungi                               | 112       | 58       | 18         | Dunn and Reynolds                |
| Vascular plants                     | 123       | 97       | 48         | Lamberson                        |
| Forams and non-plantonic Protozoans | 279       | 144      | 58         | Chave and Devaney                |
| Porifera                            | 40        | 33       | 26         | Devaney                          |
| Actiniaria                          | 27        | 21       | 14         | Cutress and Arneson              |
| Octocorallia                        | 31        | 17       | 12         | Devaney                          |
| Scleractinia (recent)               | 169       | 53       | 12         | Devaney and Lang                 |
| Scleractinia (fossils)              | 15        | 10       | 5          | Burch and Wells                  |
| Brachiopoda                         | 4         | 4        | 4          | Grant                            |
| Bryozoa                             | 84        | 61       | 39         | Cuffey and Cox                   |
| Sipuncula                           | 77        | 11       | 3          | Devaney                          |
| Echiura                             | 2         | 2        | 2          | Devaney                          |
| Platyhelminthes                     | 31        | 11       | 10         | Devaney                          |
| Nemertea                            | 1         | 1        | 1          | Devaney                          |
| Nematoda                            | 1         | 1        | 1          | Devaney                          |
| Polychaeta                          | 132       | 110      | 34         | Devaney and Bailey-Brock         |
| Mollusca                            | 1,240     | 453      | 151        | Kay and Johnson                  |
| Insects and related                 |           |          |            |                                  |
| Arthropods                          | 190       | 157      | 93         | Samuelson and Nishida            |
| Pycnogonida                         | 5         | 4        | 4          | Child                            |
| Stomatopoda                         | 12        | 4        | 4          | Reaka and Manning                |
| Cirrepedia                          | 10        | 7        | 6          | Titgen                           |
| Lagoon plankton                     | 285       | 177      | 82         | Devaney                          |
| Ostracoda                           | 10        | 10       | 5          | Kornicker                        |
| Crustacea decapods                  | Devaney   |          |            |                                  |
| Natantia                            | 145       | 56       | 14         | Devaney and Bruce                |
| Repantia                            | 4         | 3        | 3          | Devaney                          |
| Anomura                             | 76        | 29       | 10         | Hart, Haig and Knudsen           |
| Brachyura                           | 293       | 114      | 16         | Hart, Haig and Knudsen           |
| Holothuroidea                       | 20        | 11       | 5          | Cutress and Rowe                 |
| Other Echinodermata                 | 97        | 65       | 32         | Devaney                          |
| Protochordates                      | Eldredge  |          |            |                                  |
| Fishes                              | 815       | 338      | 92         | Randall and Randall              |
| Reptilia                            | 9         | 9        | 5          | Lamberson                        |
| Aves                                | 41        | 27       | 12         | Berger                           |
| Mammalia                            | 9         | 7        | 6          | Reese                            |
| Miscellaneous taxa                  | 109       | 77       | 35         | Burch                            |
| Totals                              | 4,736     | 2,288    | 902        |                                  |

Bikini Atoll to the east, and lower than species totals at Majuro and Arno atolls to the south. Most likely the high Bikini totals were due to substantially more survey and search effort (see “*Bikini Atoll, Marshall Islands*”). Coral species totals reported at the several largest islands of Palau, Yap, and Chuuk are also higher than at Enewetak but comparable to the Bikini levels. The Enewetak fish species totals are also much lower than those reported at Arno Atoll in the Marshall Islands, possibly due to greater rainfall and upwelling effects where the Equatorial Current meets the Equatorial Countercurrent. Moreover, certain groups of fishes common at Kwajalein Atoll are



**Enewetak Atoll, Marshall Islands, Figure 6** Robert Johannes on a reconnaissance visit at Enewetak Atoll before leading the Alpha-Helix Symbios study at Japtan Island in 1971. (Photo courtesy by James Maragos).

absent or rare at Enewetak. Contributing factors for the lower coral and fish levels may include geographic isolation of Enewetak from neighboring atolls, the reduced survey effort, and possibly the residual effects of the nuclear testing program.

The marine biological habitats and species at Enewetak Atoll are still among the most comprehensively studied in the world even though little research has been accomplished after 1985. Habitats surveyed in detail include:

- Deep lagoon biological communities
- Pinnacle and patch reefs of the deep lagoon
- Lagoon back reefs (or lagoon margins)
- Shallow passes on the perimeter reef between the northern islands
- Coralline algal ridges
- Ocean-facing fore reefs and
- Lagoon water column habitats

Other geological and ecological investigations have covered impacts of:

- Destructive storms on reefs
- Intertidal ecology
- Invertebrate coral predators (*Acanthaster*)
- Coral taxonomy
- Herbivory in sub-tidal communities
- Bioturbation in the deep lagoon including mobilization of radio-nuclides
- Fish communities, including shark assessments, fish reproduction, and recruitment
- Ciguatera fish poisoning and
- Biological communities in bomb craters and
- Upward reef growth and decline during the Pleistocene



**Enewetak Atoll, Marshall Islands, Figure 7** Coral specialists Michel Pichon (left), John Wells (center), and John Veron (right) at the Mid-Pacific Marine Laboratory-sponsored coral taxonomy workshop at Enewetak in 1976. The three specialists are deliberating over *Bikiniastrea laddi*, a coral first collected by geologist Harry Ladd at Bikini and described by John Wells. (Photo courtesy by James Maragos).

Some of the most important investigations included assessment of reef metabolism, trophic relationships, energy and materials flux, nutrient flux, calcification, and bioerosion rates of reefs by multidisciplinary teams including Odum and Odum (1955) and later (Figure 6; Johannes et al., 1972) during the Symbios/Alpha Helix expedition at Japtan Reef. In 1976, a coral reef taxonomy workshop was convened at Enewetak under the guidance of John Wells (Figure 7). Terrestrial environments have also been surveyed including soils, vegetation, reptiles, seabirds, shorebirds, insects, mammals, crustaceans, and other arthropods. Several islands along the southwest perimeter were also proposed as reserves and were in excellent health and mostly removed from the nuclear testing sites at the atoll.

### Summary and Conclusions

During a 40-year period, Enewetak served as World War II battleground, a U.S. nuclear testing proving ground, and an important atoll field station for marine scientists including geologists, biologists, and ecologists. The world's longest atoll drill cores were collected there and led to the confirmation of Darwin's subsidence theory on atoll evolution and documented the long history of living reefs among the world's largest and oldest atolls. However, the Enewetak people, who likely lived at the atoll for thousands of years, suffered greatly during the same time period and struggled against a world power to return home. Of all the questions left unanswered will be the fate of the people, the impact of the past nuclear testing on their atoll, and the uncertain future of both during the climate now beginning wash up on her shores.

Hopefully, scientists, governments, and islander residents alike will continue to cooperate and work towards a better understanding of the future while never forgetting the past. In one respect, the Enewetak people were able to return to their home atoll because it was not the first to be assaulted, and was larger and better able to withstand the impacts of the nuclear era vis-à-vis Bikini Atoll. In early 2009, Bikini was nominated for World Heritage as a cultural site for similar reasons that the Hiroshima Dome of Japan was recently inscribed – so that the World will never forget the role that her people and atoll played during the emerging nuclear age, the hardships they suffered, and the future lesson that such history should never be forgotten and repeated. The decision on the nomination will be made within a year. Perhaps soon Enewetak will be similarly recognized for its role and success in demonstrating how her people were able to return home and survive against great odds and serve as inspiration for others.

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Atolls  
 Bikini Atoll, Marshall Islands  
 Darwin, Charles (1809–1882)  
 Funafuti Atoll  
 Geomorphic Zonation  
 Lagoon Circulation  
 Microatoll  
 Midway Atoll (Hawaiian Archipelago)  
 Moating  
 Mururoa Atoll  
 Pacific Coral Reefs: An Introduction  
 Patch Reefs: Lidar Morphometric Analysis  
 Reef Drilling  
 Subsidence Hypothesis of Reef Development

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## ENGINEERING ON CORAL REEFS WITH EMPHASIS ON PACIFIC REEFS

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### Definition

Engineering: design, planning, construction, and management of machinery, roads, causeways, buildings, bridges, docks, airfields, fortifications, waterways, power generation, water supply, waste discharge, etc.

### Introduction

The European renaissance and industrial revolution ushered in an era of unprecedented advances in, and global demand for, modern engineering and construction capability. Five centuries ago, European explorers traveled far from home, coming into contact with many coral reefs for the first time, and requiring engineering that focused

on improved means of navigation, transportation, safe overseas anchorages, and later on conquest, commerce, communications, and trade with many cultures in coral reef environments. By the mid nineteenth century, emphasis shifted toward resource exploitation and colonization of overseas continents and islands, including guano and phosphate extraction at many coral islands and atolls, and mining of valued ores and expansion of plantation agriculture and ranching at many larger tropical islands and sub-continents. By the mid twentieth century, engineering in coral reef environments focused on supporting modern global warfare, nuclear weapons testing, and civil works for emerging democratic states including construction of military bases, airfields and ports, urbanization, and reconstruction.

The consequence of these shifts was massive pollution and degradation of many coral reefs, especially during the past century. Only during the past half century has there been emphasis placed on minimizing the ecological impacts of engineering, coastal construction and related development. This chapter reviews past and present engineering on coral reefs and offers measures to reduce lingering effects and avoiding future environmental effects on Pacific coral reefs attributed to engineering and related construction.

### **Engineering and coastal construction requirements on coral reefs**

Generally, the four principal engineering categories on coral reefs have been: (1) dredging and excavation for navigation channels and turning basins for ships and boats; (2) discharge of fill to expand land, create airfields, harbors, and connect islands via causeways on especially smaller islands and atolls; (3) collecting or constructing armor rock for fortifying shorelines, harbor breakwaters, and onshore facilities; and (4) mining and quarrying reef blocks for concrete production and construction of buildings. The last category is covered in a companion section in the chapter on Infrastructure on Coral Reefs that includes additional case studies and expands the geographic scope of this review beyond Pacific reefs. The discharge or dumping of toxic and hazardous waste (hazmat) is beyond the scope of this review but which can result in adverse consequences to coral reefs. Assessment and remediation of hazmat sites are potentially dangerous and require specialists such as eco-toxicologists and industrial/environmental engineers at great cost. Hazmat sites can be avoided by prior planning and design that leads to proper construction, operations, and maintenance of facilities.

Coastal engineering on small Pacific low reef islands and atolls is especially needed because land areas and water supplies are limited and vulnerable to adverse seas and storm conditions. Coral rock is often very hard, especially on wave exposed reef crests which render it valuable for protecting shorelines, but its extraction often requires heavy equipment or use of explosives in zones of heavy surf that drives up the cost of the shore protection.

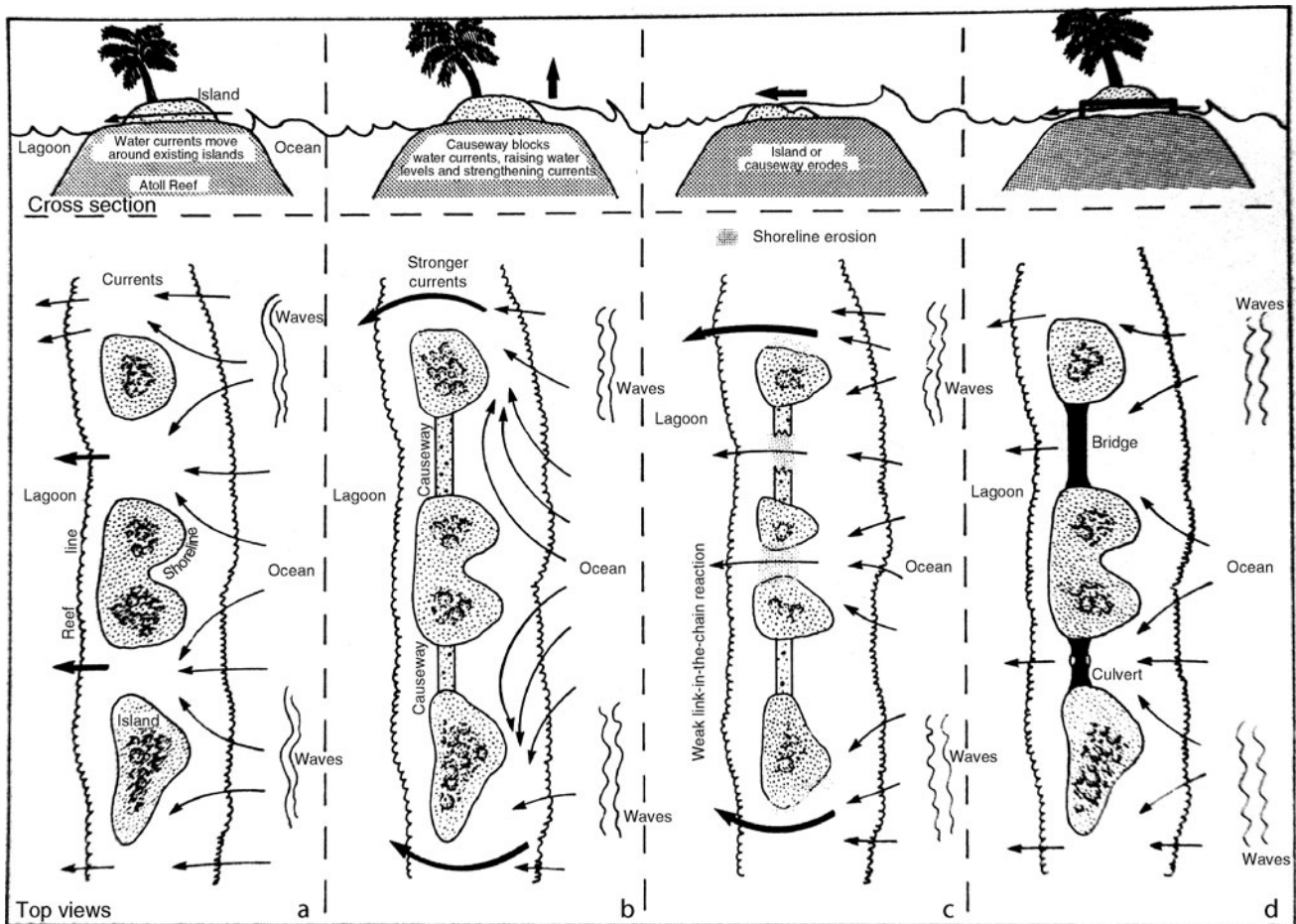
A common alternative to moving and placing large stones is using smaller, portable stones or rubble that can be carried by hand to fill up larger fish traps or wire-meshed cubes (gabions) previously placed on the shoreline. The rock-filled traps or gabions simulate the benefit of larger individual stones that better withstand movement and the erosive force of wave action and currents. Additional traps or gabions are later placed atop one another to create a seawall or sloping revetment along the shoreline. The advantages of this approach are that heavy equipment, blasting or quarrying of larger stone are not required. One disadvantage is that the wire meshing is not permanent and eventually corrodes, abrades or fails, reducing the structure to amorphous rock piles or ridges with reduced capacity to protect shorelines unless the wire mesh structures are routinely replaced. Furthermore, the shorelines where smaller stones and rubble are collected may be exposed to greater levels of erosion.

Improperly placed or designed shore protection structures of any kind eventually reverts back to shoreline erosion and the continuous need for more reef rock, rubble, and other forms of general purpose fill for repairs and haphazard shore protection. Continued excavation of coral sand and rock is also common at population and government centers in response to population immigration, especially from outer islands. As populations grow, additional coral rock and fill are needed for living areas, shore protection, dwellings, and road causeways connecting neighboring settlement islands on atolls. However, insufficient baseline studies and inadequate design have caused many road causeways to fail (Figure 1) or degrade adjacent reef areas (Figure 2) especially on atolls and barrier reefs.

WWII military bases on atolls also required road causeways to establish defensive perimeters, gun emplacements, shore protection, airfields, seaplane landing areas, protected harbors, and dredged navigation channels, if natural passes were absent. Inadequate width of channels, turning areas for ships, and aids to navigation at hastily constructed WWII-era harbors have also led to degraded reefs, many ship groundings, loss of fuel and supplies, loss of life, and the spread of alien and invasive marine and terrestrial species. Inadequate culverts or bridge openings in fill causeways connecting adjacent islands often led to shoreline erosion and failure of causeways at both military and civilian atolls and islands, disrupting land access and communications between adjacent islands. Many of these effects can be mitigated through proper engineering and related oceanographic assessment of wave energy, currents, and tidal fluctuations. Table 1 summarizes engineering activities, equipment, and construction purposes at coral reefs.

### **Adverse ecological consequences of poorly designed engineering activities and structures**

Serious direct effects to reefs can result from dredging, other forms of excavation, and discharge of fill on reefs to create land. Filling reefs to create land represents a permanent loss of the buried reefs as well as additional

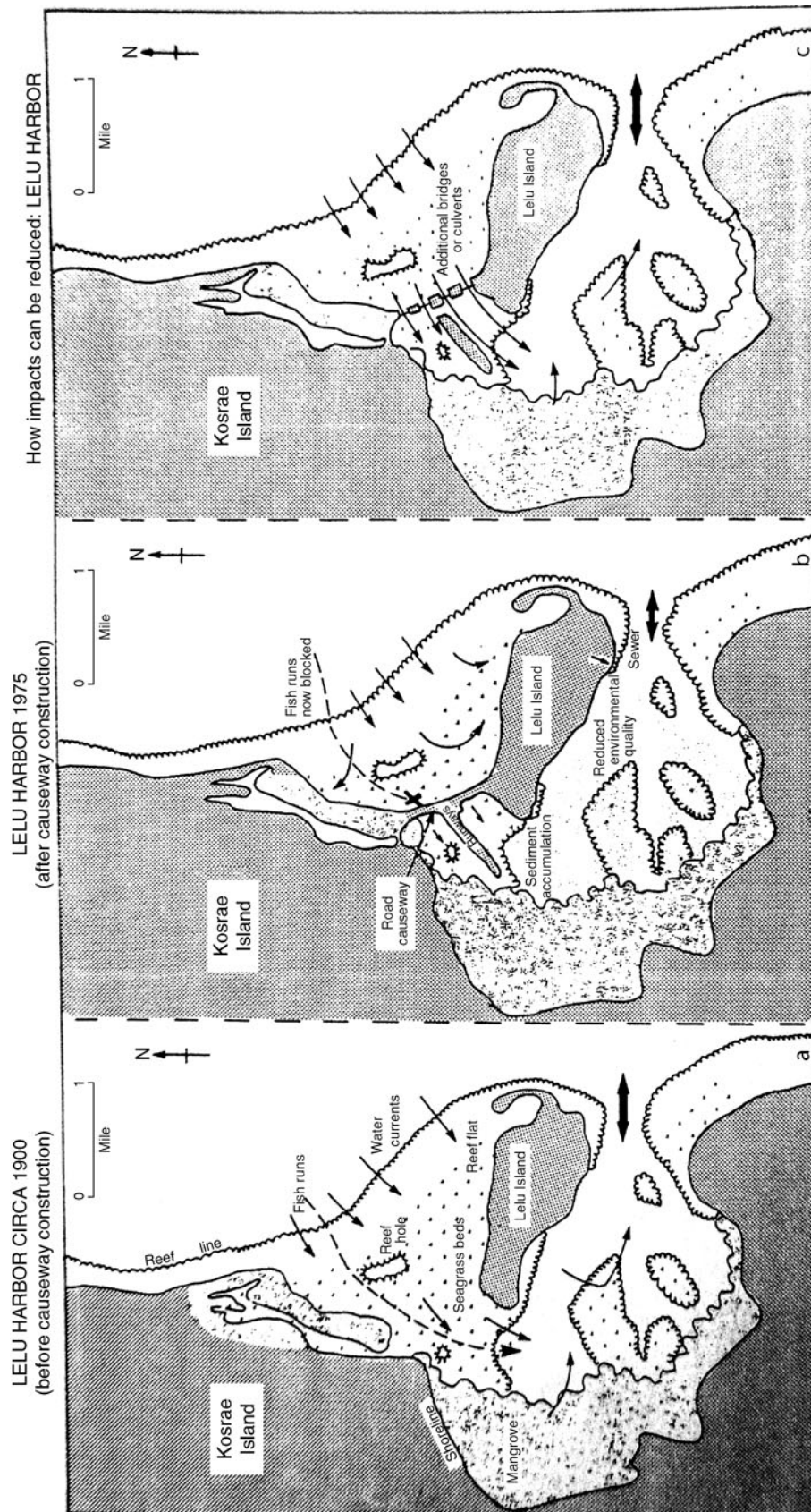


**Engineering on Coral Reefs with Emphasis on Pacific Reefs, Figure 1** Adverse consequences of poorly engineered causeways on coral reefs: (a) Reef flat before construction with wave action driving waters into the lagoon between islets. (b) Fill causeways connect islets but block flow and raise water levels. (c) High waves and seas breach causeways, preventing road access between islets. (d) Culverts or bridges in causeways maintain lower water levels, preventing causeway failures (all figures after Carpenter and Maragos, 1989; Maragos, 1993 except as otherwise indicated).

injury to reefs at the excavation/dredging sites and reefs adjacent to the fill areas. Fill areas not properly protected by filter cloth, revetments or seawalls may fail, releasing sediments, chemicals, and corroded metallic debris that are carried to healthy reefs, expanding the area of injury to healthy reefs. These types of impacts have been documented at French Frigate Shoals (Hawaii) and Palmyra Atoll (Line Islands). Limited sources of fill for residential areas and garbage landfills have degraded reefs and adjacent residential areas at Majuro Atoll and Ebeye Island (Marshall Islands) and Tarawa Atoll (Gilbert Islands). In one example at Kosrae Island, revetment stone and filter cloth was placed before discharge of fill material for an airfield that greatly reduced impacts to adjacent reefs (Figure 3). Designing shore protection structures on reefs often requires engineers to think beyond standard civil engineering practices and to consider options that reduce reef and operational impacts.

Road causeways constructed to connect the islands at southern Tarawa and islands north of Ebeye (Kwajalein Atoll, Marshall Islands) have breached with expensive repairs constantly required (Figure 1). Meanwhile the road causeways at these two atolls and at Palmyra have disrupted lagoon circulation, increased lagoon water temperatures, and caused shoreline erosion. Injury from WWII constructed road causeways at Palmyra are now degrading ocean reefs, and its lagoon reefs remain essentially dead even after 70 years since causeway construction (Figure 4). Road causeways at the larger volcanic islands of Kosrae Island, and Pou Bay at Weno Island (Chuuk, Caroline Islands) have also restricted water exchange in lagoons, blocked fish migrations, contaminated marine waters, and degraded reef areas. Installation of larger standard culverts at Pou Bay led to better water exchange and recovery of reef areas (Figure 5).





**Engineering on Coral Reefs with Emphasis on Pacific Reefs, Figure 2** Adverse effects of causeway construction between Lelu and Kosrae islands: (a) Before causeway construction, fish runs, seagrass beds, a lagoon, a deep reef hole, and offshore reef habitats thrived and supported the main population center at Lelu Island. (b) After causeway construction, water exchange and fish runs deteriorated; confounding the problem was the haphazard construction of a second causeway for an airfield that blocked one of the two culverts of the main causeway, exacerbating pollution and sedimentation in the harbor. (c) The main culvert could be un-blocked and additional culverts installed to restore fish runs and the quality of coral reefs and seagrass habitats.

**Engineering on Coral Reefs with Emphasis on Pacific Reefs, Table 1** Summary of engineering and construction techniques used on coral reefs (after Maragos, 1993)

| Category   | Activity                      | Equipment/designs                                                                                                                                             | Purpose                                                                                                                                 |
|------------|-------------------------------|---------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------|
| Excavation | Quarrying                     | Explosives<br>Drill rigs<br>Rippers and back hoes<br>Excavators and dozers                                                                                    | Obtain design stone, aggregate, and armor rock or rip-rap for coastal fortifications                                                    |
|            | Sand mining                   | Crane-operated dragline or bucket dredge<br>Floating crane-operated<br>Clamshell dredge<br>Cutterhead dredge                                                  | Remove accumulating sediment from harbor basins and channels                                                                            |
|            | Dredging                      | All the above, plus<br>Hopper dredge<br>Auger platforms<br>Explosives                                                                                         | Same as above, plus fill land expansion, road causeways, construction rock, and aggregate fill                                          |
| Filling    | Temporary causeways and dikes | Dump trucks<br>Front-end loaders<br>Cranes, dozers<br>Manual placement                                                                                        | Provide access for construction workers, confine sediment generated by construction, lay outfalls and pipes, and place shore protection |
|            | Fill land creation            | All of the above, plus<br>Crane-operated dragline or Bucket dredge,<br>Suction & cutterhead dredge<br>Graders, rollers, compactors<br>Seawalls & sheet piling | Expand land areas for roads, airfields, urban development, resorts, other buildings, berthing in harbors                                |
|            | Coastal structures            | Crane-operated clamshells<br>Wire cages or gabions<br>Manual placement<br>Front-end loaders                                                                   | Shore protection<br>Beach restoration<br>Flood control, navigation wave energy dissipation                                              |

Additional indirect adverse effects to adjacent reefs are often more severe when ship channels dredged through atoll perimeter reefs:

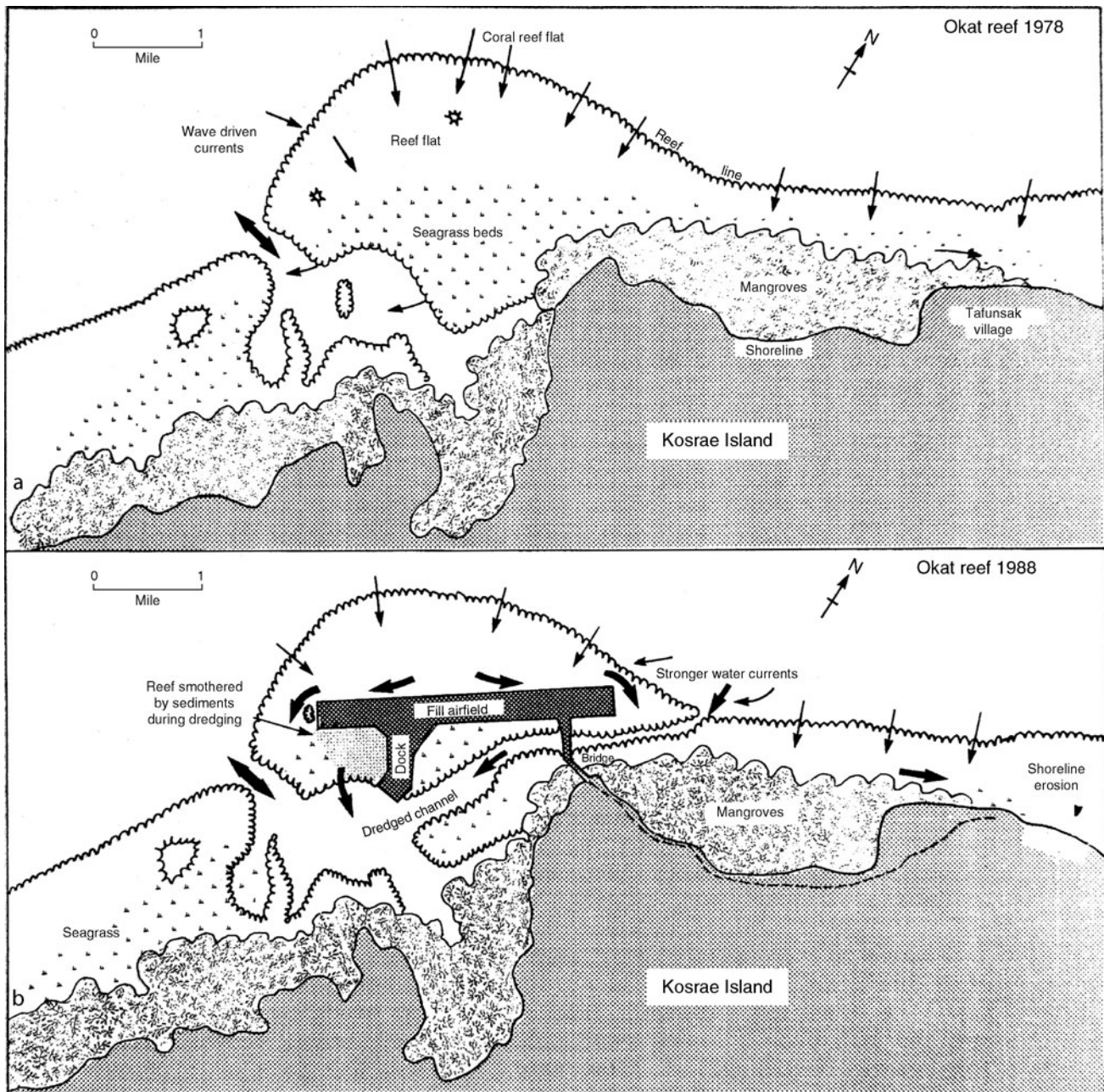
- Fine sediments are stirred up on lagoon floors
- Lagoon waters become stratified
- Reef crests are permanently exposed to air
- Lagoon and ocean reef habitats are degraded
- Water circulation between ocean and lagoon habitats is reduced (Figure 6)

Irreparable impacts to coral reefs have been documented at U.S. Navy installations constructed before and during WWII at several atolls and islands in the central Pacific: Pearl Harbor; French Frigate Shoals; Midway Atoll; Kāne'ohe Bay (Figure 7); Johnston Atoll; Palmyra Atoll; Kiritimati Atoll; Wake Atoll; and Kanton Atoll. Also, 1960 airfield constructed at Tutu'ila Island (American Samoa) blocked circulation at neighboring Pala Lagoon that killed corals, degraded water quality and mangroves, and caused shoreline erosion at nearby villages (Figure 8). Harbors not properly designed may also invite ship collisions and groundings as has also occurred at Pearl Harbor and Palmyra Atoll. The reefs of Baker Island (Phoenix Islands) have also been degraded at an anchorage where extensive war materiel was dumped and vessels scuttled immediately offshore before the troops left the island. Alternatively, harbors placed inland from the

shoreline reduce impacts to coral reefs at small boat and deep draft harbors in Hawaii (Figure 9).

Engineering and construction projects that do not address long-term trends and the indirect impacts of population growth and crowding on coral reef islands are also bound to fail. For example, the U.S. Army missile testing center at Kwajalein Atoll has not adequately addressed the impact of population growth at Ebeye stimulated by more than a thousand workers who commute daily to the neighboring military base at Kwajalein Island. In essence, Ebeye has become a "border town" outside the jurisdiction of the military base, but with the local government lacking long-range plans and funds for water supply, sanitation, garbage, and health care deficiencies at Ebeye. The reefs and resort areas on Maui and Waikiki (Hawaii) and Denarau (Vanua Levu, Fiji) have also suffered from myopic decision-making by government engineers and planners. Continuous beach replenishment is now required at Waikiki and seawalls have replaced the once beautiful beaches at Denarau because the hotels were allowed to be constructed too close to the ocean, putting them in harms way during high seas and storm conditions. An airfield placed offshore from Kuta Beach in Bali permanently destroyed much of the beach and could have been avoided by moving it behind the shoreline (Figure 10).

Maui (Hawaii) resorts and the local government needed better planning and support for an ocean outfall to

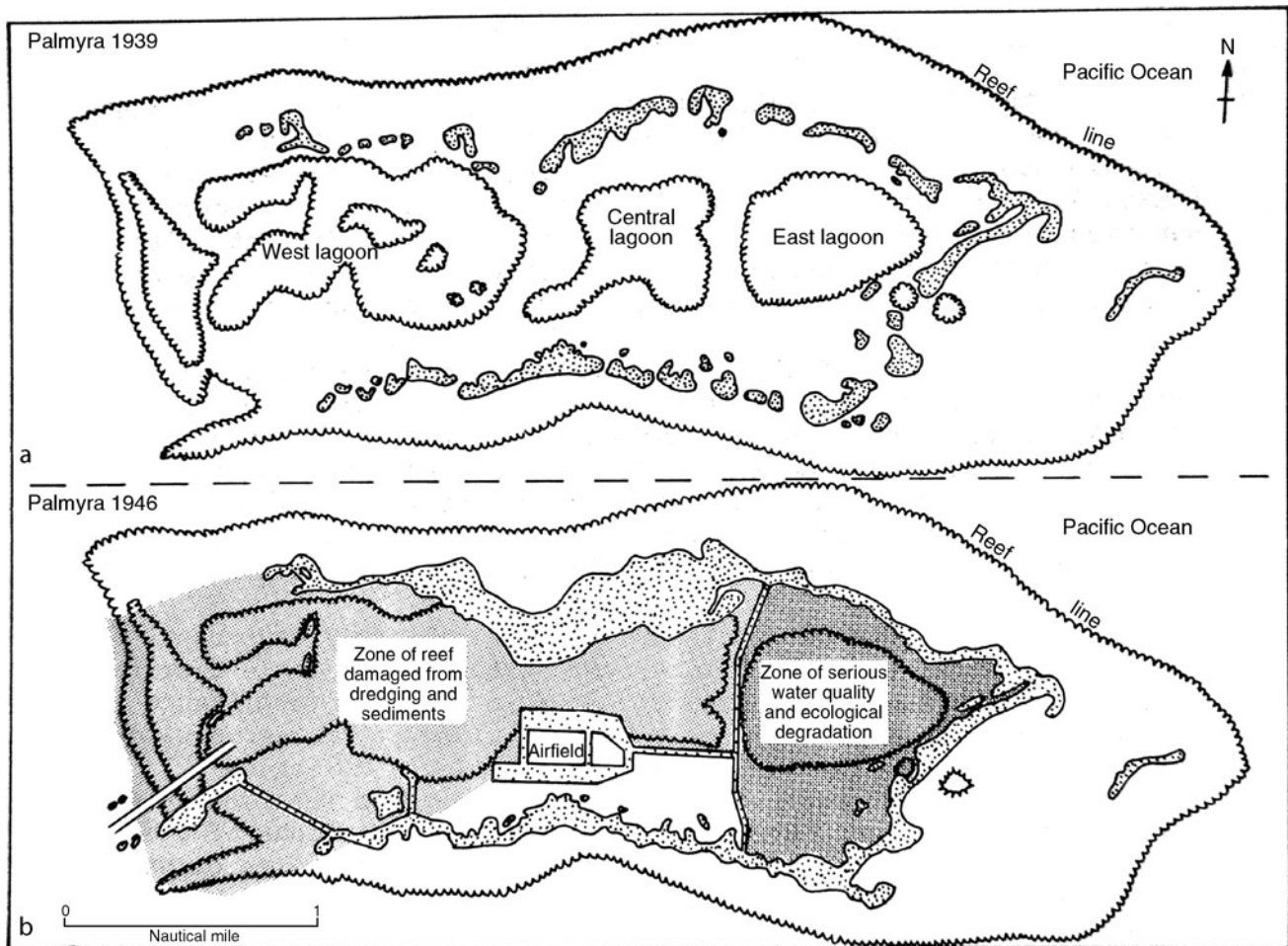


**Engineering on Coral Reefs with Emphasis on Pacific Reefs, Figure 3** Mitigating the effects of dredging and filling to construct a reef runway and dock at Okat, Kosrae: (a) Okat supports the largest natural bay, seagrass beds, estuary, coral reefs and mangroves in Kosrae. (b) The original construction plan proposed cutter-head dredging to generate and stockpile fill material for the dock and airfield. However, the construction contractor was required to construct a free standing revetment around the perimeter of the airfield and install filter cloth to block discharge of dredged materials outside the airfield. The changed revetment design spared destruction of adjacent reefs and prevented undermining and failure of the airfield from strong wave-driven currents since its completion in 1980.

discharge treated sewage offshore and away from beaches and coral reefs near the resorts. Instead sewage is still discharged into groundwater via injection wells, resulting in higher nutrient concentrations that seep into the ocean

at the shoreline, resulting in prolific algae growths stimulated by the nutrients. In turn the algae smother offshore coral reefs and accumulate as drifts on the beaches that require constant collection and disposal to maintain





**Engineering on Coral Reefs with Emphasis on Pacific Reefs, Figure 4** Adverse effects from Naval Air Station construction at Palmyra Atoll, U.S. Line Islands: (a) Before 1938 Palmyra Atoll and its 50 emerald islets was called the “Pearl of the Pacific.” (b) Before WWII the U.S. Navy dredged a channel through the perimeter reef, lowering lagoon water levels and cleared a seaplane landing area. The fill was used to connect the islets and construct road causeway around the perimeter of the atoll and expand land areas for a harbor and airfield. The construction immediately destroyed all reef life in East lagoon and eventually the entire lagoon. Later breaching of causeways and the synergistic effect of a coral bleaching event in 1997 degraded coral gardens west of the lagoon and now threaten coral gardens on eastern reefs. After 70 years there has been no reef recovery in the lagoon, although restoration plans are now being developed (Figure after Dawson, 1959).

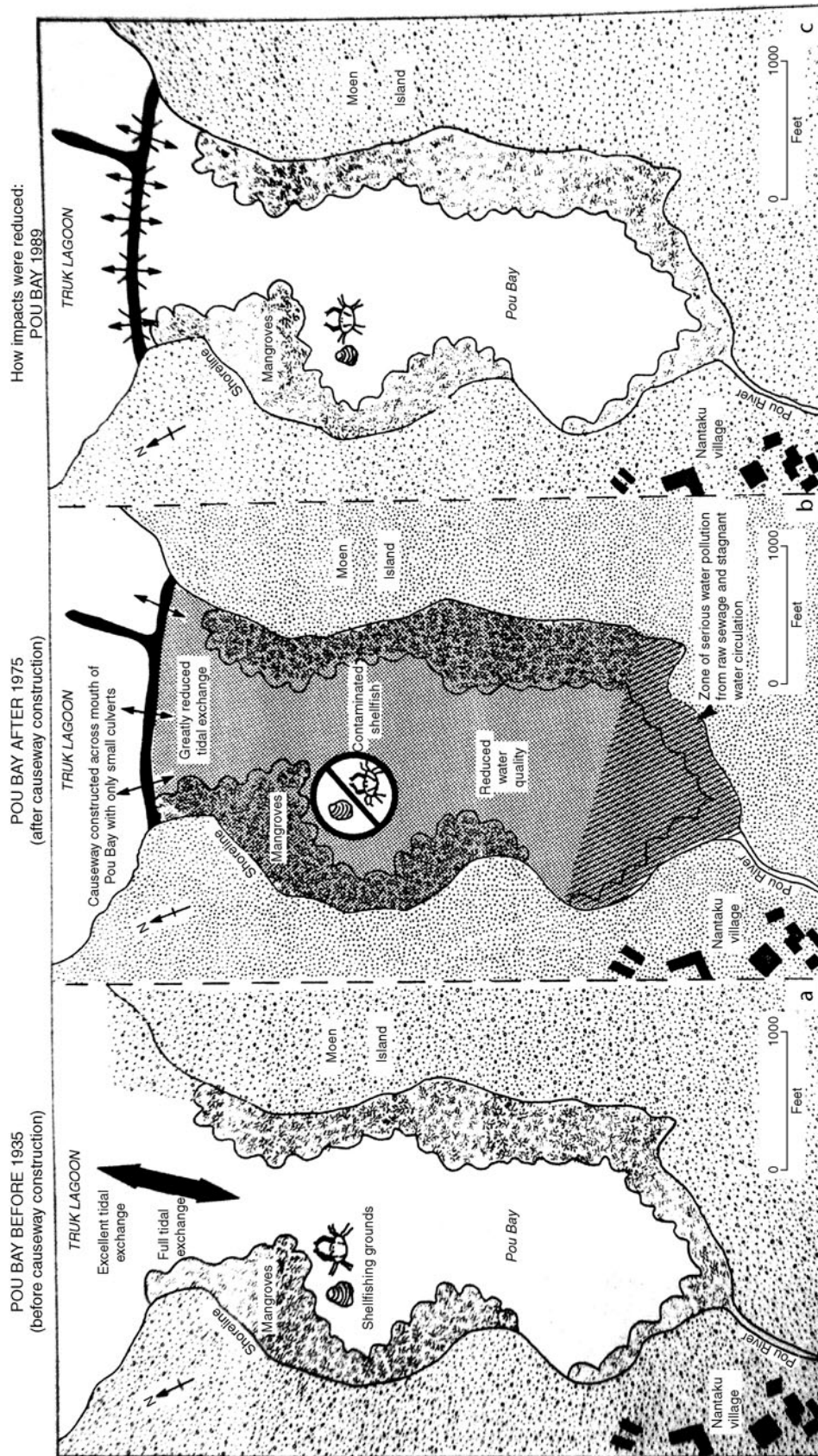
aesthetics. Meanwhile the government and resorts continue to hire consultants to study and debate the dilemma.

Sewage discharges in the lagoon of Kāneʻohe Bay (Hawaii) in the 1960s resulted in decline of corals and proliferation of green algae stimulated by nutrients in the sewage that were overgrowing and smothering corals. After 1968–1972 ecological studies demonstrated the adverse effects of the sewage, government and community leaders agreed to move the sewage outfall to a deeper site outside the lagoon in 1977–1978 where wave energy dissipated and diluted the sewage and caused only minor effects to coral reefs (Figure 7). Subsequent lagoon surveys in 1983 and 1997 in the Bay revealed the recovery of coral and decline of the invasive green algae. Additional

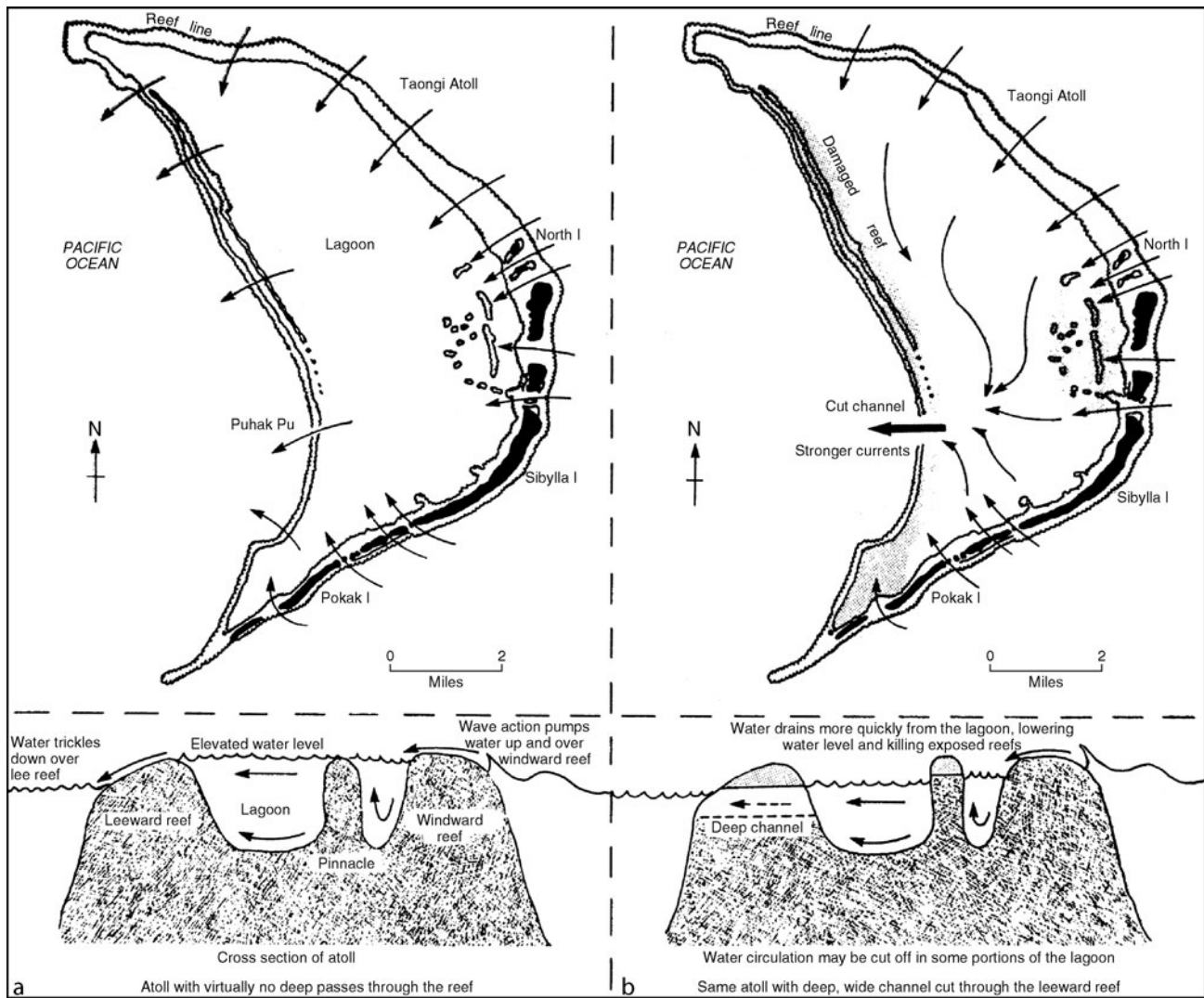
surveys were accomplished in the Bay in 2009, revealing further declines in green algae but the rise of alien red algae (Nadiera Sukhraj, pers. comm.).

### Summary

- Planning teams should be assembled before engineering plans and specifications are approved and include engineers, scientists, planners, economists, and members of the affected communities.
- Governments should adopt and require Environmental Impact Assessment (EIA) procedures and coordination before decisions are made.
- The EIA process should include: public scoping of issues; baseline ecological, oceanographic and cultural



**Engineering on Coral Reefs with Emphasis on Pacific Reefs, Figure 5** The fall and rise of the estuary and coral reefs in Pou Bay, Chuuk Lagoon from 1935–1980: (a) Before 1935 Pou bay was a productive estuary, mangrove forest, seagrass bed, and shellfish bed with adjacent villagers dependent on it for subsistence. (b) Then the Japanese built a road causeway across the mouth of the bay that polluted and degraded the ecosystem because culverts placed through the causeway were inadequate in size and number. (c) Mandated by U.S. environmental laws and regulation, reconstruction of the causeway required installation of larger culverts which in turn helped restore the bay's marine ecosystems by 1980.

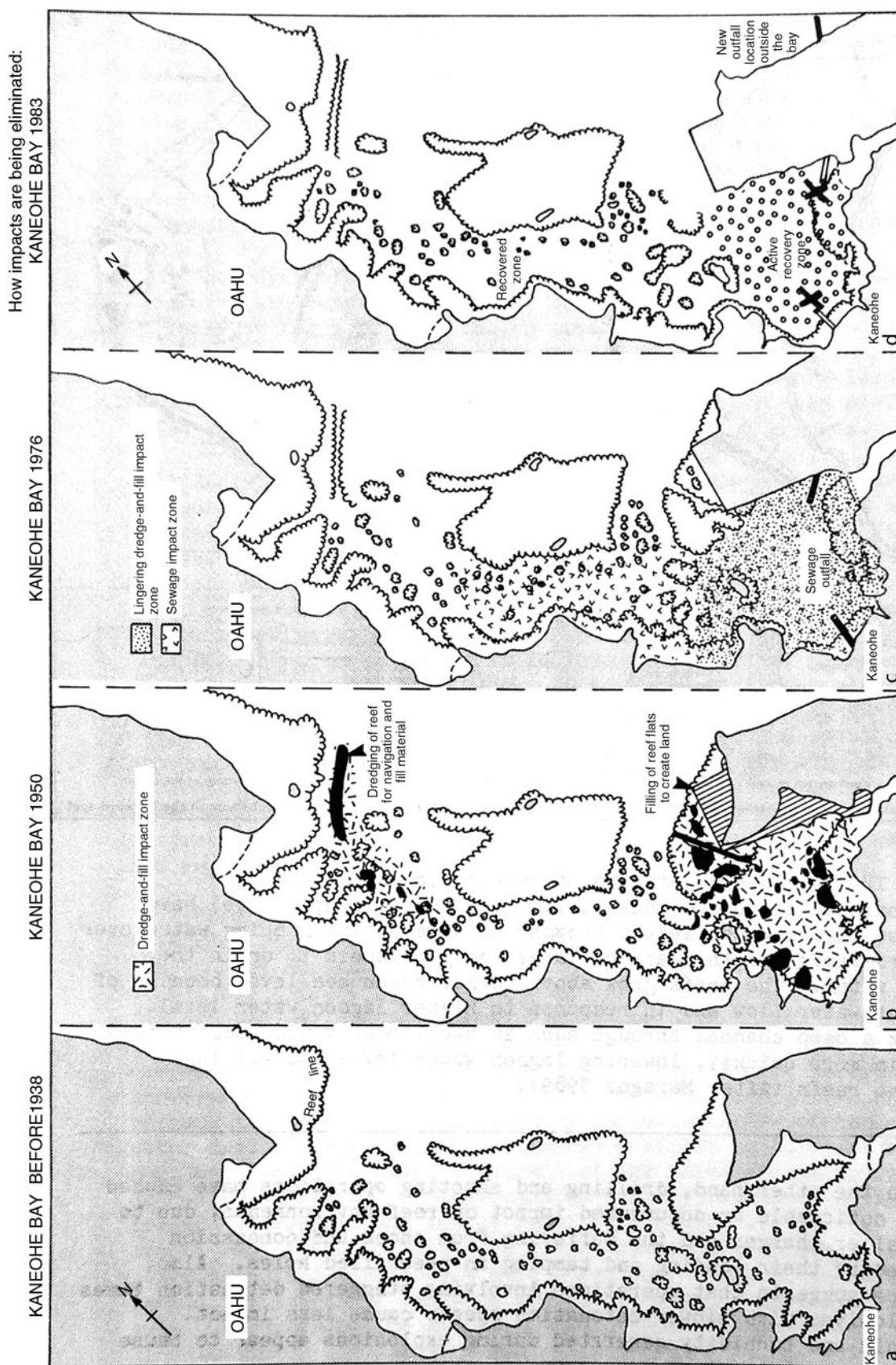


**Engineering on Coral Reefs with Emphasis on Pacific Reefs, Figure 6** Adverse impact of boat and ship channels cut into lagoons lacking deep natural passes: (a) Numerous atolls lack adequate discharge from natural passes to match inflow from tides and wave action. Experiencing constant water flow, perimeter reef crests continue to grow upwards and lagoon water levels rise above adjacent ocean water levels at low tide. (b) Large or deep ship channels cut through perimeter reefs drains excess lagoon waters, exposes perimeter and lagoon reefs to the air, kills corals and other reef life, permanently modifies deep lagoon circulation, and perpetually stirs up fine, often colloidal, bottom sediments.

- surveys and analyses; evaluation of a full range of alternative sites and designs; and evaluation of a full range of measures to reduce or avoid adverse impacts.
- The final decisions of the EIA should be incorporated into the construction plans and specifications in the form of an Environmental Protection Plan that the construction contractor(s) must honor.
- The EIA process should require an environmental audit of the completed project to address impacts not covered or anticipated in the pre-project phase of the EIA.

- The project area should be monitored by an independent team of scientists and engineers who report construction violations or issues directly to the government contracting officer who in turn has the authority to suspend the construction until deficiencies are corrected.
- Use of explosives should include measures to reduce damage to adjacent reefs by (1) drilling holes to load smaller charges and (2) covering each detonation site with heavy cloth to reduce fly-rock, concussion and shock to marine life.

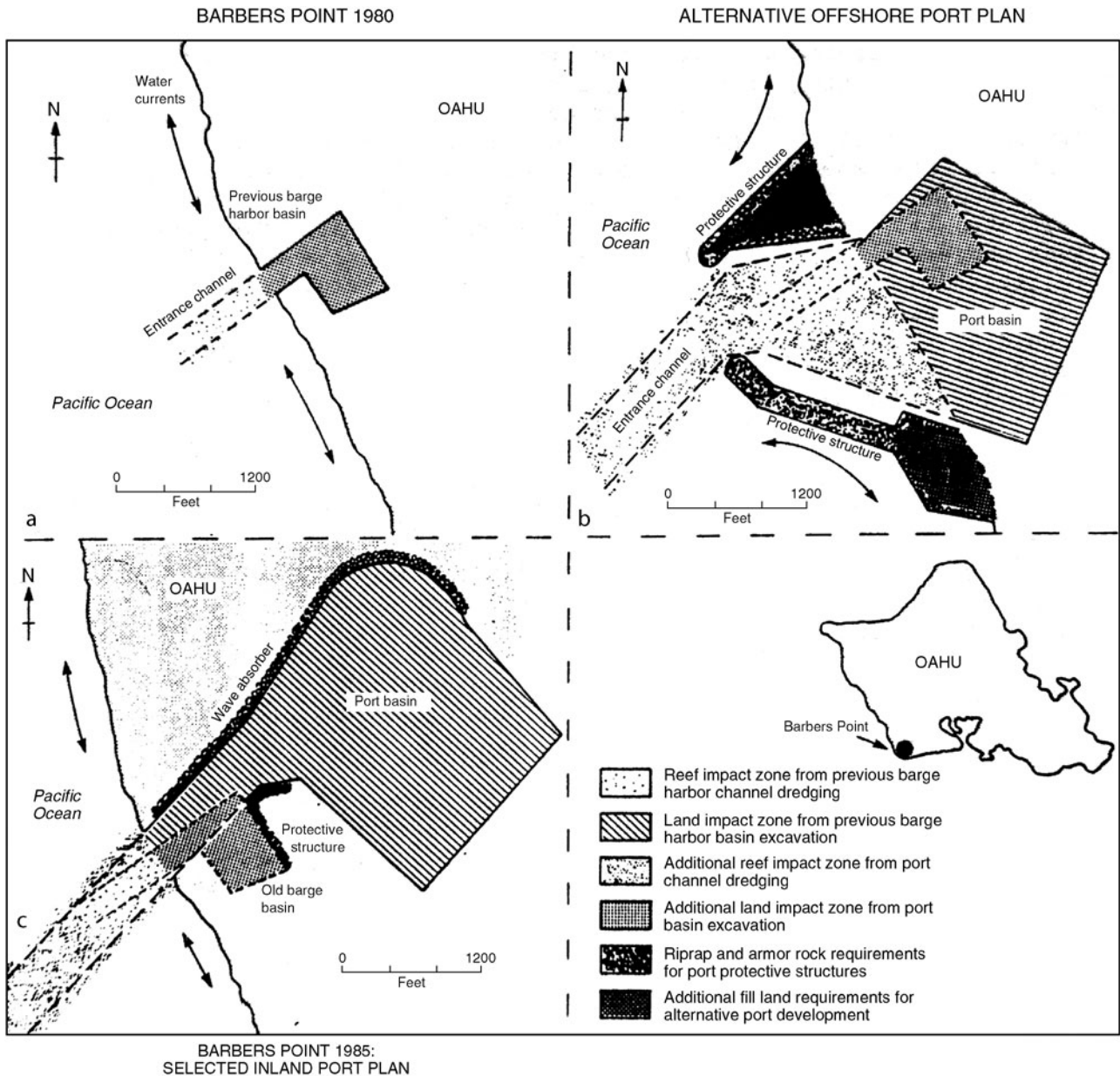




**Engineering on Coral Reefs with Emphasis on Pacific Reefs, Figure 7** Adverse planning of military construction and sewage discharge in Kaneohe Bay, Hawaii: (a) Before 1938, Kaneohe Bay was an undisturbed healthy ecosystem, supporting one of two barrier reefs in the Hawaiian Islands. (b) WWII military construction dredged a seaplane landing area and deep ship channels through the barrier reef and lagoon, and created fill land for the military base using dredged coral. (c) In the early 1960s sewage outfalls were placed in the south bay where water circulation was poor, causing pollution, killing corals, and stimulating algal overgrowth of corals in the lagoon. (d) Outfalls were moved outside the bay by 1978, resulting in coral recovery and decline of algal overgrowth by 1983, with the new outfall was placed in well-mixed ocean waters offshore where reefs were unaffected. Additional surveys through 2009 revealed the disappearance of the earlier algae and spread of new alien algae released in the bay by researchers that now threaten rare corals.



**Engineering on Coral Reefs with Emphasis on Pacific Reefs, Figure 8** Adverse consequences of poor planning and design of airfield construction on reefs: (a) Pala Lagoon in American Samoa before airfield construction was home to lagoon reefs, rare mangroves, and shellfish beds of importance to adjacent Nu'uuli villagers. (b) Fill for airfield construction was placed too close to the entrance of the lagoon, reducing circulation, creating lethal water temperatures, killing reef life, eroding nearby beaches, contaminating shellfish, and polluting waters near the village. (c) Had EIA procedures been required a decade earlier, an alternative of placing the airfield on land would have avoided all these impacts and reduced construction and maintenance cost.

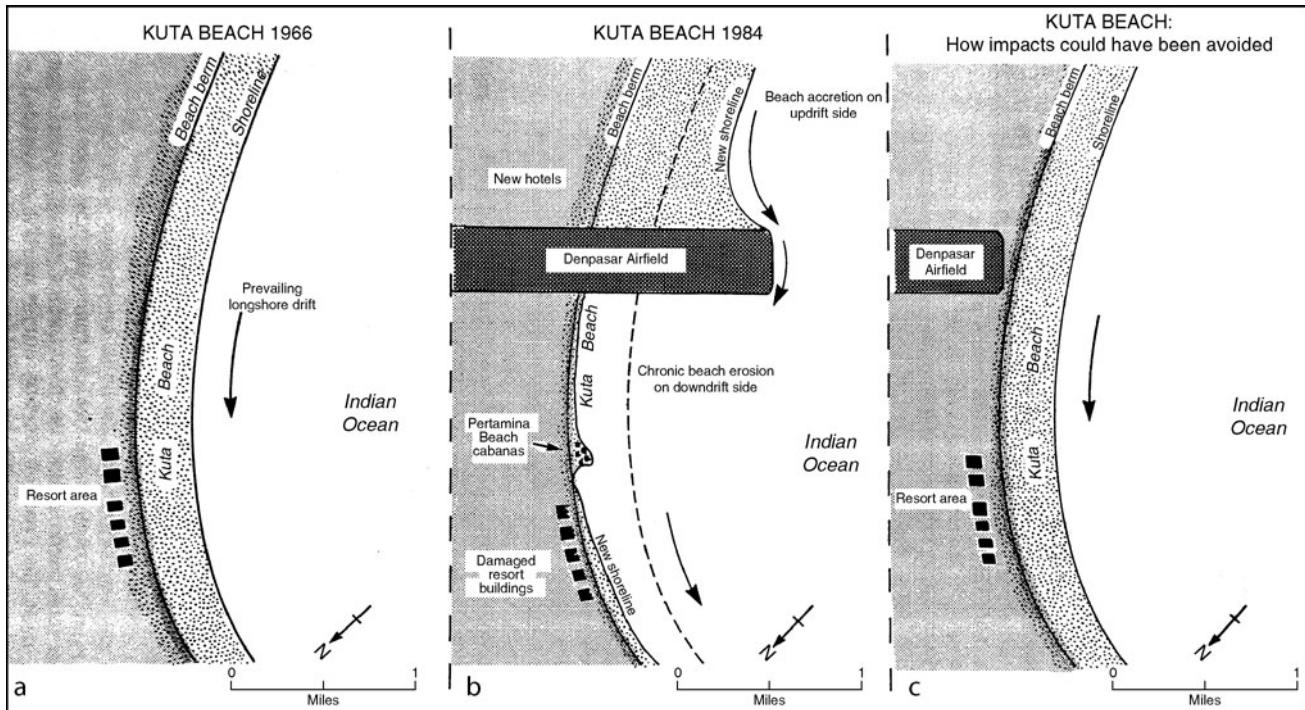


**Engineering on Coral Reefs with Emphasis on Pacific Reefs, Figure 9** Port construction at Barbers Point, Hawaii designed to minimize impacts to coral reefs: (a) Before harbor construction in 1980, U.S. environmental laws and regulations required evaluation of a full range of alternatives. (b) The two major options were to construct the harbor offshore, or . . . . . (c) Quarry a harbor inshore of the existing shoreline. The latter option was selected, and all excavation in the new harbor basin, and channel dredging outside were completed before the barrier separating the two areas was removed to complete the harbor. This design minimized the footprint of the harbor on coral reefs and also prevented turbid waters from discharging to offshore reefs during most of the construction period. The project cost was also much less and generated fill material for future industrial and construction projects.

- Nations with coral reefs should design a coastal zone management (CZM) regime that (1) allows only projects and facilities that need to be placed in the coastal zone, and (2) establish greenbelts and other restricted zones to protect beaches, mangroves, and coral reefs and prevent resorts or other building development in

this restricted zone unless absolutely required. This measure alone would save many existing beaches and prevent proliferation of seawalls and groins to protect luxury housing and other structures that could have been sited elsewhere and out of harms way from storms, high waves, tsunamis, etc.





**Engineering on Coral Reefs with Emphasis on Pacific Reefs, Figure 10** Airport construction destroys Kuta Beach at Denpasar, Bali: (a) Kuta Beach in Denpasar, was Bali's most important tourism destination before 1967. (b) Requiring a modern airfield to support increasing tourism, the government opted to extend much of the runway offshore to minimize the high cost of purchasing land for the rest of the airport. After construction, the offshore end of the runway functioned as a giant groin that trapped sand flow from south to north along the beach, causing the north side of the beach to erode away, and destroying many adjacent residences and businesses. (c) Had the decision-makers consulted ocean engineers and scientists, they would have been aware of the beach impacts and the corresponding socio-economic costs of placing the runway in the beach. Instead they may have opted for the alternative of placing the entire runway well behind the beach.

- Dredging and filling methods and plans for projects should require reduction of turbidity and sedimentation or confining both to the immediate construction sites to protect adjacent reefs.
- Other mitigation methods should be evaluated such as coral transplantation that may also help reefs recover from previous impacts from sediments and dredging.

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## Cross-references

Atolls  
 Conservation and Marine Protection Areas  
 Infrastructure and Reef Islands  
 Lagoon Circulation  
 Midway Atoll (Hawaiian Archipelago)  
 Nutrient Pollution/Eutrophication  
 Pacific Coral Reefs: An Introduction  
 Sediments, Properties  
 Wave Set-Up  
 Waves and Wave-Driven Currents

## EOLIANITE

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## Synonyms

Aeolianite (United Kingdom); Dunerock (South Africa); Grès dunaire (Mediterranean); Miliolite (India, Middle East); Kurkar (Israel)

## Definition

Eolianites are cemented sand dunes created by the processes of entrainment, transportation, and deposition on land, by wind. The accumulated dune sands are subsequently altered by various geochemical processes in a meteoric (freshwater) environment. Most eolianites have a high carbonate content, with clasts made up of whole/fragments of marine skeletons, *ooliths*, and peloids. Carbonate eolianites are commonly found in sub-tropical to tropical coastal locations. Silica- or lithic-dominated eolianites tend to be found in drylands or in more temperate environments. Most recognized eolianites in the landscape are Quaternary in age. Few examples of pre-Quaternary eolianites exist and this is thought to be due to misinterpretation of these deposits rather than to their absence from the stratigraphic record.

The grains making up siliciclastic eolianites are normally coarse silt to sand-sized, well-sorted, and rounded. In comparison, carbonate dunes contain a wider range of clast-size and -shape because the carbonate grains have a lower specific gravity (Frébourg et al., 2008) and some skeletal fragments are platy in nature, which enable larger clasts to be wind-entrained. Bedding structures include cross-bedding and laminations, which represent the progradation and extension of the dunes. Dune slipfaces are identifiable as steeply dipping laminae up to 30–34°. In terms of thickness, eolianites vary from <1 m to >100 m.

The mineralogical changes associated with the *diagenesis* of eolianites include the alteration of unstable high-Mg *calcite* and *aragonite* and precipitation of relatively stable low-Mg *calcite*. Dissolution of aragonitic shells and *ooids* often results in molds with fossil outlines preserved by micritic envelopes. Both air and water fill pore spaces in the vadose zone giving unevenly distributed cement patterns. Meniscus, rim, and pore-filling cements occur with crystal size normally ranging between 5 and 50 µm in diameter and crystal shape typically being bladed, equant, or syntaxial. Cement sources include dissolution of bioclasts, *ooids*, peloids, and carbonate-rich lithoclasts, terrigenous dust, seaspray, leaching of overlying sands, and precipitation from groundwater or overland flow (McLaren, 2007). Karstification or *palaeosols* may develop at/above major unconformities in eolianites and in semi-arid environments *calcretes* can develop because of processes of carbonate dissolution and rapid reprecipitation.

Relative *dating* techniques attempted to establish the age of dunes/eolianites include lithostratigraphy, human artefacts, and amino acid racemization. Of the numerical techniques, uranium-series *dating* on shells is problematic as they often behave as geochemically open systems. Radiocarbon *dating* requires organic matter to be present in the dunes and only dates back to ~50 ka. Luminescence *dating* of terrigenous grains has successfully obtained ages ranging from a few decades to several hundred thousand years.

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## Cross-references

Aragonite  
 Calcite  
 Calcrete/Caliche  
 Diagenesis  
 Electron Spin Resonance Dating (ESR)  
 Micrite  
 Ooids  
 Palaeosols

# F

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## FAROES REEFS

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### Synonyms

Basin reefs; Faros; Little ring-shaped reefs; Mini-atolls;  
Miniature atolls

*Faro* is a Maldivian name given to small atolls that rise in the lagoons of large composite atolls, or, are found on their rims (Agassiz, 1902). Despite his vast experience of coral reefs in the Pacific and Caribbean, Agassiz (Agassiz, Alexander (1835–1910)) said he had “seen nothing so striking” as “those remarkable rings which are so characteristic a feature in Maldivian coral reef scenery”. Classical faros are indeed striking, being perfectly circular reefs, usually less than 3 or 4 km in diameter surrounding a shallow secondary lagoon of depths generally less than 20 m. To J. S. Gardiner (Gardiner, John Stanley (1872–1946)) such reefs were technically “little atolls” but where a more precise term was necessary, he borrowed *faro* and *velu* from the Maldivian, the former signifying a small ring-shaped reef and the latter its central pond or basin.

Because faros rise from the lagoon floor and edges of atolls, their mode of formation must differ from oceanic atolls whose foundations extend to great ocean depths. And yet there has been no substantive study of faros in the *Maldives*, which contrary to popular belief do not occur throughout the archipelago but are restricted to the double chain of atolls in its central part, where there are several hundred faros. The occurrence of circular or oval faros within the lagoons appears to be related to two

factors: the presence of frequent or wide gaps or passes through the atoll rim; and, to the alternating northeast and southwest monsoons with reversals in swell and sea waves and locally generated wind waves. Faros developed on the peripheral rims themselves are rarely circular or even occluded. Rather they are often elongated parallel to the atoll edge, or are crescent- or horseshoe-shaped with the convex side facing the open sea.

A number of faro reefs are surmounted by islands, whose shape frequently mimics that of the parent reef. Some islands are restricted to parts of the reef rim, especially on faro with deep velu. In other cases, infill from sediments produced on the reef surface and transported into the velu results in centrally located, often circular islands (Kench et al., 2005).

While reefs that resemble Maldivian faros have been described from elsewhere including Indonesian waters, the northern Great Barrier Reef, and New Caledonia, the terms *faro* and *velu* should be limited to reefs in the Maldives. Moreover, faros *sensu strictu* are not to be confused with either micro atolls (*Microatoll*) or “oceanic faros”.

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### Cross-references

[Atolls](#)  
[Maldives](#)  
[Patch Reefs: Lidar Morphometric Analysis](#)



## FLOATSTONE

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Floatstone is a type of limestone which displays 10% or more of the grains larger than 2 mm in diameter and there is mud (matrix) between the grains (like packstone – sand sized).

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## FLORIDA KEYS

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## Synonyms

Asymmetric reef-tract evolution; Calcified organisms; Cemented oolitic tidal bars; Cumulative coral reefs; Emergent reefal and oolitic limestone; Florida Keys National Marine Sanctuary; Holocene *Acropora palmata*; Inhabited island chain off south Florida; Key Largo Limestone; Miami Limestone; Outlier reefs; Pleistocene *Montastraea annularis*; Replicated antecedent facies and geomorphic landforms; Shallow south Florida shelf; Windward platform-margin rim

## Definitions

**Quaternary:** The Quaternary Period consists of the Pleistocene and Holocene Epochs, the most recent ages of geologic time. The Pleistocene ranged from ~1.8 Ma to 10 ka. The Holocene began at 10 ka and includes the present. On the basis of glacial/interglacial intervals as determined by oxygen-isotope analyses of fossil planktic foraminifera, the Quaternary has been divided into numbered Marine Isotope Stages (MISs). Even numbers represent glacial intervals: relative to the Florida Keys reef record, MIS 10, 8, 6, 4, and 2 are pertinent. Interglacial intervals are referred to as MIS 11, 9, 7, 5, 3, and 1, with MIS 1 being the present warm interlude. MIS 5 is subdivided into substages 5e through 5a. Coral ages show that Florida Keys reefs flourished during transgressive and regressive intervals immediately surrounding late Quaternary sea-level maxima at ~230 (MIS 7), 125 (MIS 5e), 112 (MIS 5d), 106 (MIS 5c), 92 (MIS 5b), and 80 ka (MIS 5a) (Muhs, 2002; Lidz et al., 2007). The highest stand among those maxima occurred at ~125 ka when the sea level was ~10.6 m higher than at present. Conditions then produced the now emergent fossil coral reef (Key Largo Limestone; Multer et al., 2002) and tidal-bar

oolite (Miami Limestone; Hoffmeister et al., 1967), which comprise islands of the Florida Keys.

**Q Units:** Quaternary marine sequences in the Florida Key Largo Limestone have been divided into Q1 (oldest) through Q5 (youngest) Units (Perkins, 1977). The first flourishing reef occurs in the Q3 Unit. The oldest Q3 corals (*Montastraea annularis*), cored in the upper Keys, have been dated to ~370 and 366 ka (Multer et al., 2002). Those authors and others (e.g., Muhs et al., 2003) correlate those ages to the highstand of MIS 9. However, some authors (e.g., Droxler et al., 2003a) argue that the Q3 reef could belong to MIS 11. The MIS 11 highstand was the highest (~20–25 m higher than at present) and longest (30–40 kyr duration) in the Quaternary (see papers in Droxler et al., 2003b).

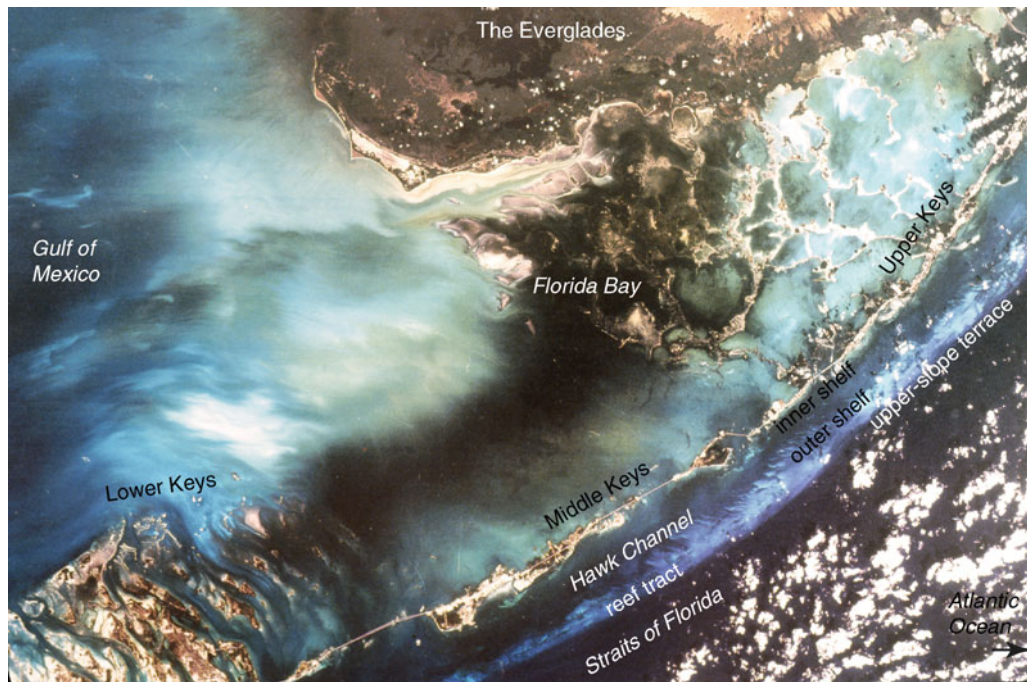
**Mangrove peat:** Modern mangrove forests and calm water rim the Florida Keys. The forests form peat, a compacted accumulation of partially decomposed organic debris. Dates on and depths of Holocene peat recovered from beneath offshore coral reefs provide times of peat formation and positions of paleoshorelines relative to the present sea level. Peat presence implies quiescent conditions at those sites during formation. Higher elevation outer-shelf bedrock topography protected those sites from waves as sea level rose. The deepest Keys mangrove peat cored was recovered from ~15 m below the present sea level (Lidz et al., 1985).

**Bedrock:** Researchers regard the uneven Pleistocene limestone surface on the south Florida shelf as “bedrock.” Wherever bedrock in contact with overlying Holocene coral reefs and sands has been dated, the dates point to the highstand of 80 ka (Lidz, 2006).

**Ooids/oolite:** Ooids are concentric grains of calcium carbonate that precipitate in warm, highly agitated seawater. During the 125-ka highstand when the Key Largo Limestone reef was growing, seaward-flowing platform-interior waters piled up behind the reef, causing high-energy convergence zones around its northeastern and southwestern ends. Ooids formed in these zones and amassed as unstable tidal bars. With sea withdrawal, the exposed bars became cemented into (Miami Limestone) oolite.

## Geographic and geomorphic setting

The Florida Peninsula, located at the southeast corner of the continental United States, is the emergent part of a broad, shallow, southward-extending carbonate platform. Seawater (Gulf of Mexico, Straits of Florida, Atlantic Ocean) surrounds the peninsula to the west, south, and east (Figure 1). The Florida Keys form a discontinuous island chain trending west–southwest from the southern peninsular tip. The submerged bedrock ~5–7 km seaward of the Keys is Pleistocene, generally <12 m deep (Enos and Perkins, 1977), and harbors the largest coral reef ecosystem in the contiguous United States. Several meters deeper to the southwest than northeast, the shelf curves westward into the Gulf of Mexico where its shallow



**Florida Keys, Figure 1** Enhanced Thematic Mapper Plus image, acquired in May 2000 from the Landsat 7 satellite, shows the four geographic components of the South Florida Ecosystem: the Everglades (south part), Florida Bay, the Florida Keys, and the reef tract. Note anastomosing shallow-water mud banks in Florida Bay. Endangered mangroves fringe every visible shoreline. The upper and middle Florida Keys are an emergent 125-ka coral reef. The lower Keys are emergent ooid tidal bars of the same age. Seaward of the keys lie habitats of the inner shelf, Hawk Channel, sands, and Holocene reefs on the shallow outer shelf, and 30-m-high 80-ka fossil reefs at the shelf edge. The Gulf of Mexico is at left, Straits of Florida at right. Pre-existing topography and fluctuations in sea level were the primary controls on coral reef evolution and distribution.

depths terminate at the west end of a bedrock ridge known as the Marquesas–Quicksands ridge (Figure 2a). Farther west, the shelf underlies Holocene reefs and islands of the Dry Tortugas. Holocene flooding from southwest to northeast produced older reefs to the southwest. Most Keys reefs occupy water depths of ~3–30 m.

Bedrock topography controls major geomorphic elements: a depression under Florida Bay, the Florida Keys, an inner shelf, a depression beneath Hawk Channel, an outer shelf, and an upper-slope terrace in 40 m of water (Lidz et al., 2006). All parallel the margin, marked by the 30-m depth contour. Orientation, composition, and tidal-pass width divide the island chain into lower, middle, and upper Keys (Figure 2b). Modern reefs, located seaward of the Keys, are healthiest off the upper Keys, which lack natural tidal passes. The least healthy occur off the middle Keys where passes are numerous and wide (Lidz and Hallock, 2000).

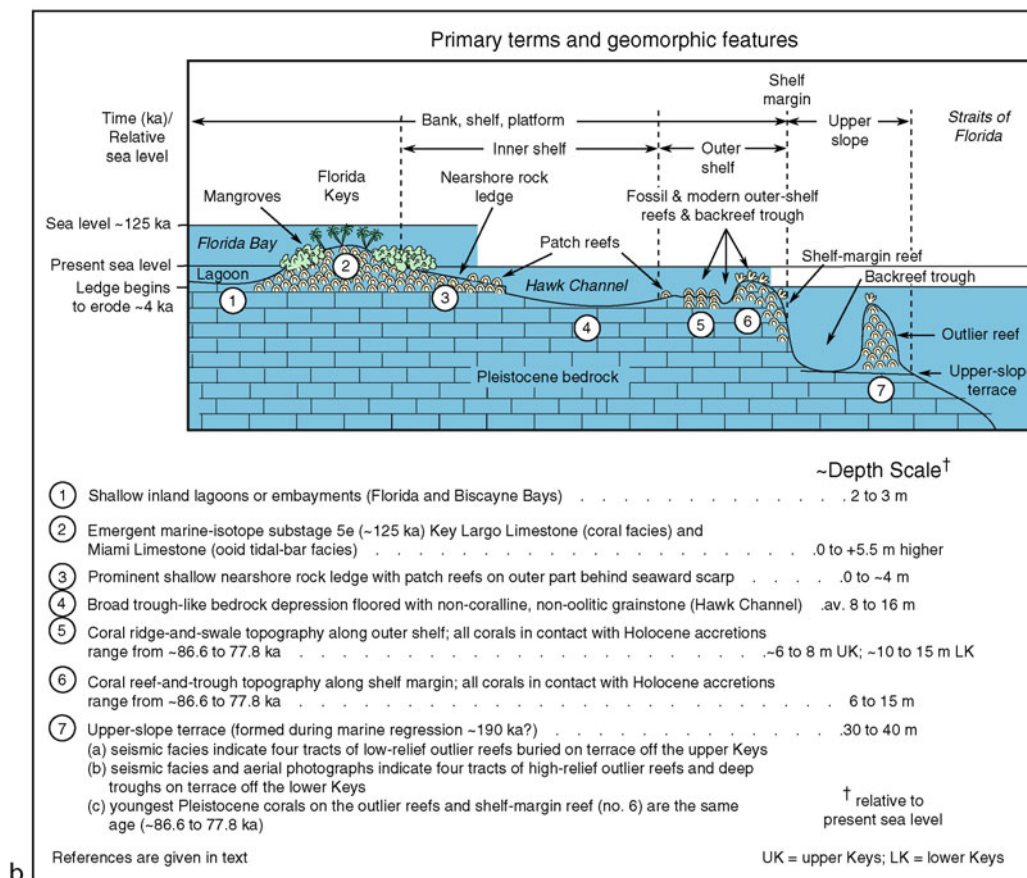
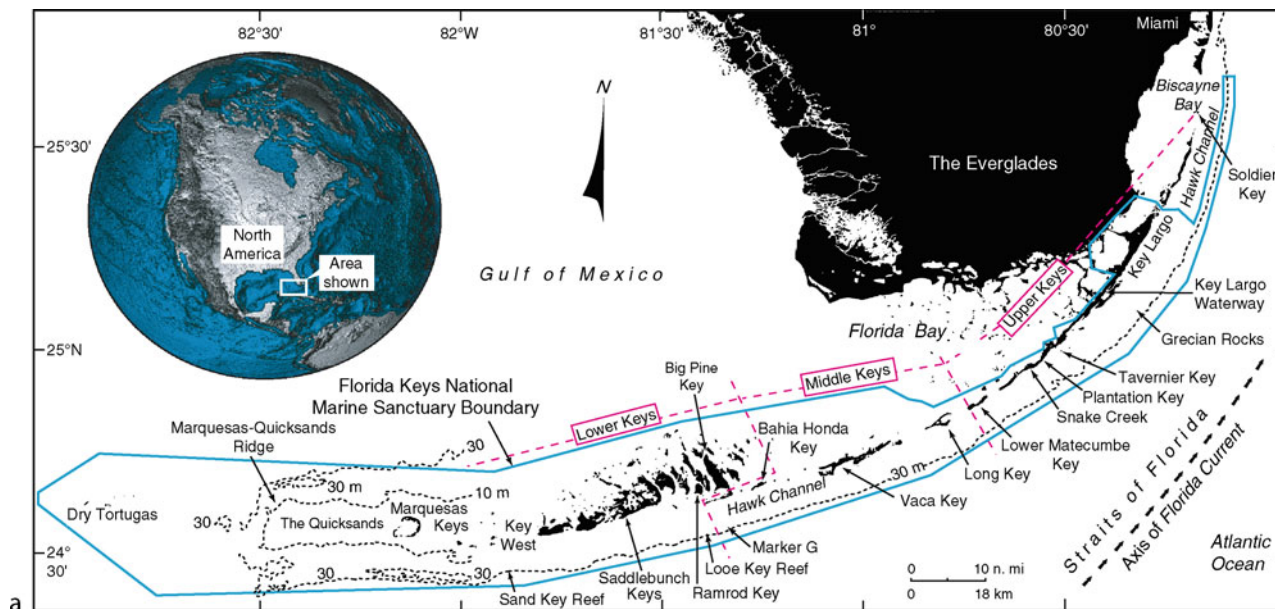
The curved Florida Keys shelf is a windward platform margin. Prevailing southeasterly winds and waves are onshore in the northeast. Shallower water and lack of tidal passes limit influence of tides and currents. Daily sediment movement is negligible. Prevailing energy is along-shore in the southwest. Deeper open-marine conditions

and wide tidal passes permit strong tidal and current exchange between the Gulf of Mexico and Florida Straits. Sediment is transported offshelf.

### Seven coral ecosystems and reef decline

Excluding corals of the Q3 Unit, about which little is conclusively known, the past 325 kyr of Florida reef evolution are well studied (cf., Lidz et al., 2008). Seismic surveys, coring, sclerochronology, and radiometric dating of coral, mangrove peat, and calcrete have shown that the two most important controls on reefs during that time were fluctuating sea level and antecedent bedrock topography (Shinn et al., 1977).

Dates on Florida Keys corals record six late Pleistocene highstands and reef ecosystems. The two highest occurred at ~125 and 80 ka. The seventh (Holocene transgression) produced the modern ecosystem. Geomorphogenetic models derived from coral dates and seismic data show the origin and changing evolution of landforms at four dissimilar sites (reef and non-reef) along the shelf edge (Lidz, 2004). The models illustrate asymmetric evolution. The seven ecosystems accrued mainly by successive stacking of new coral



**Florida Keys, Figure 2** (a) Index map of south Florida and the Florida Keys. *Dashed red dogleg line* separates areas of Pleistocene ooid bank (Miami Limestone) of the lower Keys and coral reef (Key Largo Limestone) of the westernmost middle Keys. An ooid bank also formed at the east end of the reef and today underlies the city of Miami. Note that major tidal passes are in the middle Keys. *Dotted line* (30-m depth contour) marks the shelf margin, which lies within the Florida Keys National Marine Sanctuary boundary (blue line). Figure 1a is cited in figure captions for Chapters Calcrete/Caliche, and Porosity Variability in Limestone Sequences. (b) Schematic cross section (not to scale) illustrates geomorphic features across the south Florida shelf.



generations on top of older skeletal generations. The models also show backstepping (landward coral growth) and lateral stacking (linking) of reef tracts by infilling of broad backreef troughs (Figure 3a and b). Offbank sediment accumulations extended non-reef areas seaward over lesser distances.

Coral ages indicate that the proto-Florida platform was subaerially exposed from the post-125-ka regression to ~7 ka. Though the 80-ka highstand was the last that enabled Pleistocene marine deposition on the shelf, position of the sea then only reached a maximum of ~9 m below present (Lidz, 2006). Present depths to bedrock are <9 m on most of the shelf seaward of the Keys and average ~6–8 m on the Marquesas–Quicksands ridge. Thus, the platform interior and westward-extending ridge remained dry land for ~115 kyr. During that time, the landmass promontory protected five shelf-edge reef tracts from the cold Gulf of Mexico waters (Figure 4a and b). Coastal Florida Bay waters did not exist. Geomorphic settings of the post-125-ka Pleistocene highstands provided shelf-edge accommodation space, shelter, and favorable conditions for reef calcification and accretion. Relative to the long landmass duration, the collective time of off-shore Pleistocene reef accrual was comparatively short (~20 ka; Lidz, 2006).

For unknown reasons, the Holocene transgression produced only ~2 m of coral growth on the five 80-ka shelf-edge reef tracts before the rising sea fully inundated the shelf. As the sea rose, it created and gradually submerged ephemeral islands of mangrove/mud, coral rock, and sand. At ~4 ka, seawater was far enough inland to infiltrate inter-reef paleochannels of the Key Largo Limestone, creating tidal passes that would allow saltwater access to the Florida Bay depression. During these events, outer-shelf reefs (e.g., Grecian Rocks) behind the shelf-edge reef responded by backstepping landward to keep pace with the rise (Neumann and Macintyre, 1985). Though initiated on hard substrate, some reefs also backstepped over carbonate sand and rubble (e.g., Looe Key Reef; Shinn, 1980; Lidz et al., 1985).

Then conditions changed. At ~2 ka, coastal bay and cold gulf waters began to flow seaward through the passes, impacting health of reefs opposite the passes (Porter and Porter, 2002). Terrestrial and atmospheric stressors (Jameson et al., 2002), including African dust (Shinn et al., 2000), joined the assault. Corals responded by declining, then by succumbing rapidly within the last 30 years. As of this writing (October 2008), more than 95% of Florida Keys reefs are senescent (non-accretionary), coral mortality having resulted mainly from diseases. Only small, isolated colonies of reef-building coral species are alive. Reef-framework structure is decaying due to bioerosion, ocean acidification, and natural (hurricanes) and anthropogenic (boat groundings) mechanical breakdown. Where live corals exist, underlying skeletal framework is mostly overgrown by sea fans, sea whips, algae, fleshy encrusting organisms, sponges, and stinging corals, all associated with reefs in decline.

## Two structural architectures

Florida Keys reefs consist of two repetitive architectures: a narrow low-relief outer-shelf ridge-and-swale geometry (Figure 5) and a broad high-relief shelf-edge reef-and-trough geometry (Figure 4a and b). Both are linear, discontinuous, and submerged and parallel the curved shelf edge. Cores from transects across the outer-shelf rock ridges have recovered skeletal Holocene corals overlying Pleistocene corals (Shinn et al., 1977). Cored swales contain unconsolidated Holocene sands overlying a calcrete-coated subaerial-exposure surface that caps cemented Pleistocene sands. Eight such coral ridges are visible in aerial photographs (Lidz et al., 2007). The ridge-and-swale structure is tens of meters wide and thin relative to the reefs and troughs.

The five major shelf-edge tracts form the reef-and-trough structure on a wide (~2.5 km) upper-slope terrace ~40 m below the present sea level. The landward tract is the shelf margin. The others are outlier reefs, so called because empty backreef troughs render them detached from the shelf (Lidz et al., 1991). The exposed landmass promontory protected these five tracts so well for so long that they accumulated imposing relief (~30 m). Their corals date to ~106, 94–90, and 86–77.8 ka with an inferred age of ~127 ka at their bases. Thin Holocene reefs with spurs and grooves cap these reefs. The reef-and-trough geometry is hundreds of meters wide.

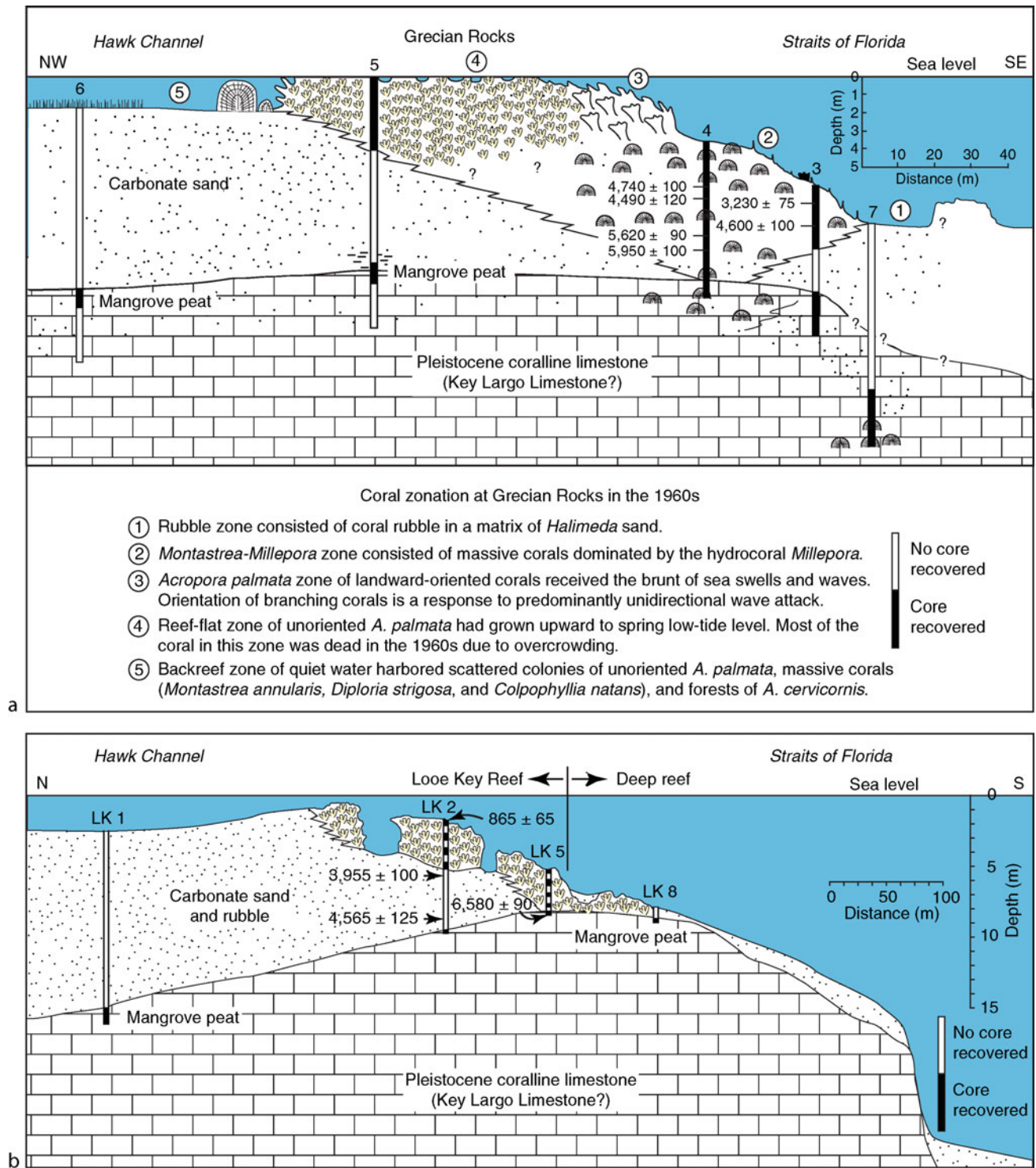
## Four coral nuclei

Pleistocene outer-shelf beach dunes, antecedent reefs, and a nearshore coral-and-oolite rock ledge are well-known coral substrates along the Florida reef tract. Ledge patch reefs, usually individual live head corals surrounded by sand halos, are in the shallowest of Keys reef settings (~3 m deep).

Thousands of patch reefs, many with coalesced halos, live in the middle of Hawk Channel, mainly off the lower Keys (Figure 4b). No geologic studies have focused on their origin, mid-channel alignment, distribution, and location. Analysis of benthic habitats and bathymetry (Lidz et al., 2006) has resolved their four-part characterization and has revealed a fourth type of coral nucleus new to the Florida record. The patches align along landward edges of two long inner-shelf bedrock troughs within the Hawk Channel depression. The troughs are presumed to consist of grainstone/wackestone, as is found elsewhere in channel bedrock (Shinn et al., 1994).

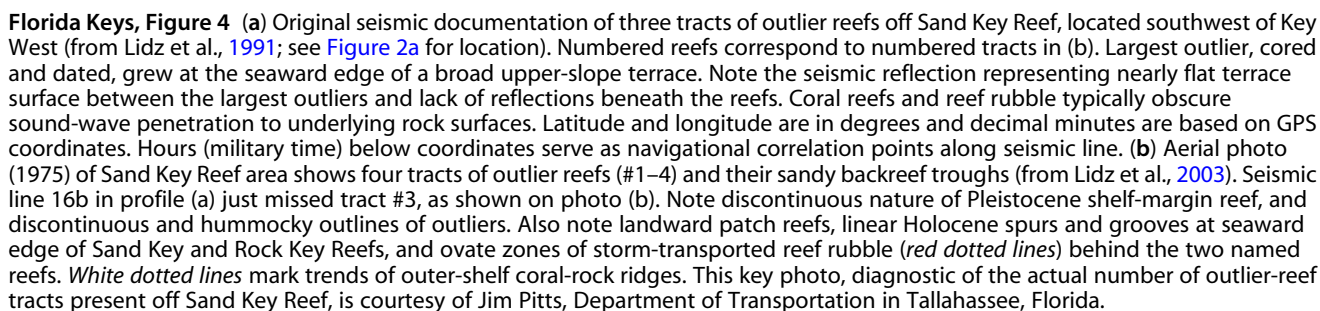
## Coral spurs and zonations

Holocene corals also formed outer-shelf patch reefs along and parallel to the shelf edge. Though linear, these reefs had seaward spur-and-groove structures in which coral spurs grew perpendicular to incoming waves (Figure 4b; see also Fig. 1 in Chapter Spurs and Grooves). The high-energy shelf-edge setting dictated that the surf-loving branching species *Acropora palmata* would build the spurs. Nearly all margin spurs consist of densely interwoven skeletal *A. palmata* (Shinn, 1963).

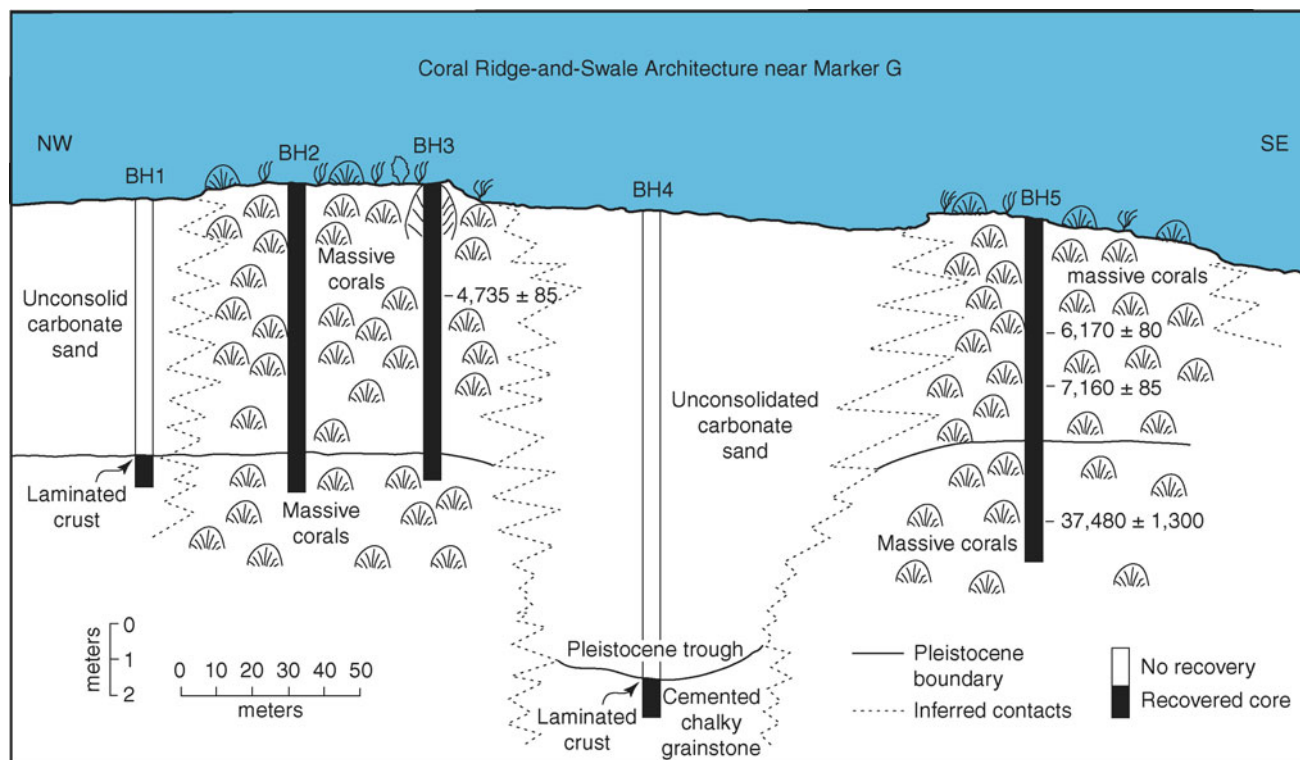


**Florida Keys, Figure 3** (a) Cross section of Grecian Rocks shows reef components and uncorrected radiocarbon ages in years before present (year B.P.) of corals recovered in cores. Coral zonation at Grecian Rocks in the 1960s showed five distinct zones. Field observations in 2002 found that most corals including hydrocorals were dead. (b) Cross section of Looe Key Reef (LK) shows that the Holocene reef began accretion on the crest of a Pleistocene topographic high. Note reefs at both sites (a and b) backstepped over carbonate sand. See Figure 2a for locations on reef tract.









**Florida Keys, Figure 5** Cross section of core transect across two rock ridges inshore from U.S. Coast Guard Marker G and southwest of Bahia Honda Key (BH) in the lower Keys (see Figure 2a for locations). Cores were labeled BH because the Bahia Honda Bridge is the only object visible from the outer-shelf core site. Cores show that the ridges are coral reefs, are growing vertically, and are separated by a sediment-filled swale. Note the lack of a Pleistocene trough on landward (NW) side of left coral ridge. Also note the uncorrected radiocarbon ages of recovered corals. The  $37,480 \pm 1,300$   $^{14}\text{C}$  date, obtained on a recrystallized coral, was thought to be much too young due to contamination with younger carbon. Inferred age of bedrock coral sections is between  $\sim 86.2$  and  $77.8$  ka (MIS 5a), which is the age range for the youngest Pleistocene corals on the shelf and for all dated Pleistocene corals in direct contact with Holocene accretions (Toscano, 1996; Multer et al., 2002; Lidz et al., 2003). MIS = Marine Isotope Stage.

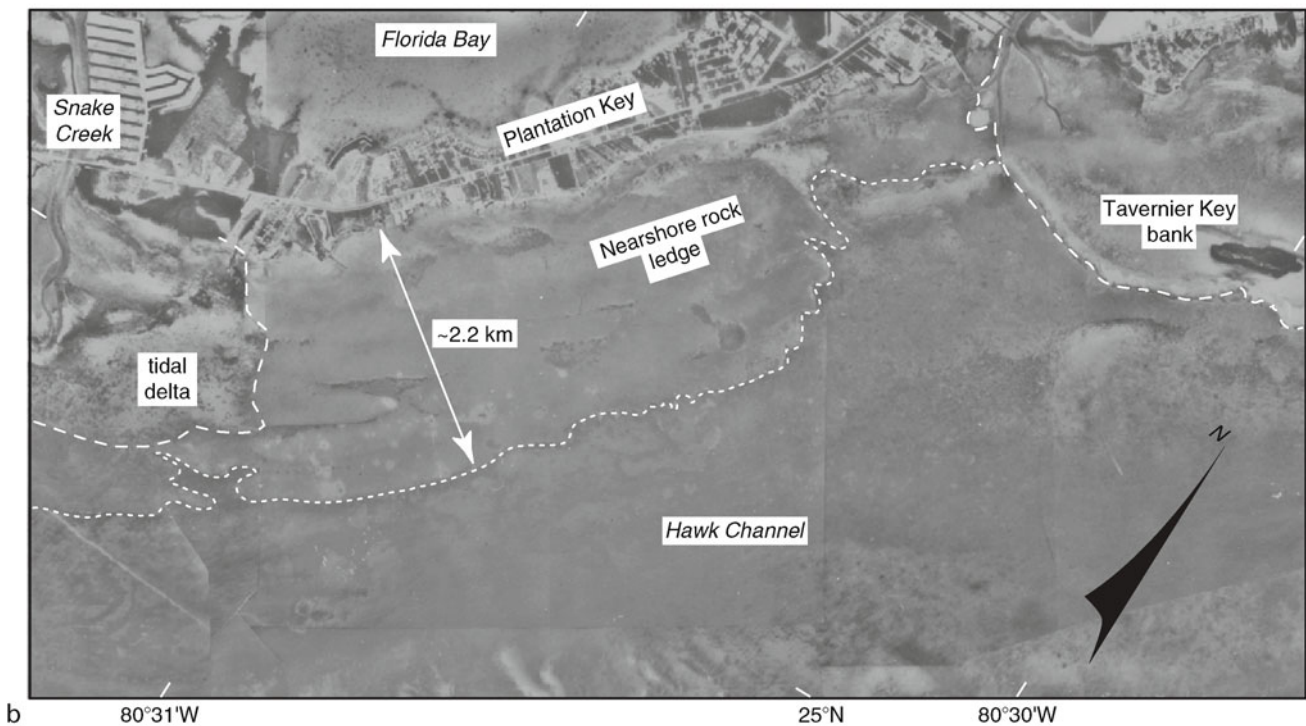
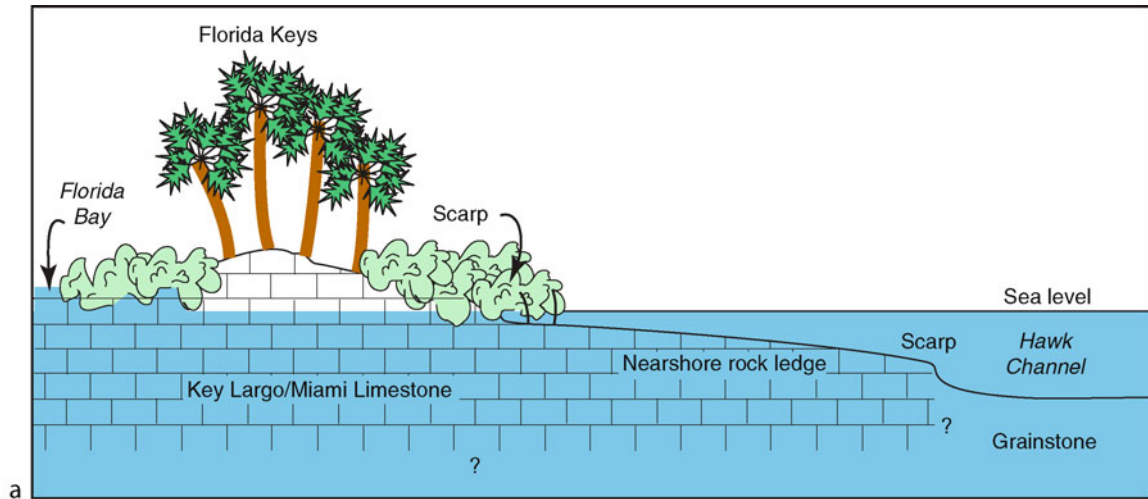
Behind the shelf edge, the spur-and-groove system consists of coral zonations (Figure 3a), features that differ from those of the pure *A. palmata* shelf-edge spurs. Zonations result from reef efforts to keep pace with both rising sea level and associated changing wave energy. Deeper water head corals, especially the boulder-coral species *Montastraea annularis*, typically first colonized this type of reef. Their skeletons now form the deepest, most seaward zone (Shinn, 1980). A shallower zone of landward-oriented *A. palmata* followed. Orientation is a response to constant unidirectional high-energy sea swells and waves. Unoriented corals cannot survive in surf because of physical breakage. The third zone is a landward reef flat with unoriented *A. palmata* that grew to spring low tide. The most landward zone is a quiet-water back reef that harbors skeletal colonies of unoriented *A. palmata*, massive species (*Montastraea annularis*, *Diploria strigosa*, and *Colpophyllia natans*), and forests of branching *A. cervicornis*. Though not necessarily of coral zonations, similar classes (fore reef, reef crest, reef flat, back reef) are found at different depths

on most Holocene outer-shelf reefs and are also present in the Holocene record on the largest and most seaward of the lower Keys outlier reefs.

The dominant type (head or branching) and species of coral skeletons in an area are proxies for ambient conditions when the corals were alive. In Florida Keys reefs, massive head corals characterize the Pleistocene, implying quiescent, protected, or deeper water. The promontory landmass was the key (protective) element. *Montastraea annularis* is the dominant species. Branching corals typify the early Holocene, implying active surf. *Acropora palmata* dominated then but is rarely found alive today.

### Key Holocene events and effects

Rising Holocene sea level generated two respective opposing processes (deposition and erosion) of different durations ( $\sim 7$  and  $\sim 4$  ka) at different locations (shelf edge and near shore). Two geomorphic structures unique to the Keys windward-margin record resulted: an



**Florida Keys, Figure 6** (a) Sketch (not to scale) shows interpreted origin of the nearshore rock ledge. (b) Aerial photomosaic (1975) shows the clearly visible ledge (*outlined in short dashes*) that lines the seaward side of all the Florida Keys. Area shown is in the upper Keys (see Figure 2a). A tidal delta at Snake Creek and a muddy bank at Tavernier Key (*long dashes*) cover parts of the ledge. Note the ledge is much wider than the adjacent island, Plantation Key. Plantation Key consists of the emergent Key Largo Limestone coral reef. Total width of ledge and island is consistent with a sloping forereef and a landward reef crest, indicating that the seaward edge of the ledge may represent the seaward extent of the Key Largo Limestone. Bedrock beneath Hawk Channel is grainstone/wackestone (Shinn et al., 1994). Thin sands cover inner part of ledge. Outer part is generally bare rock with scattered patch reefs, especially in lower Keys.

asymmetrically prograded platform and a uniformly eroded nearshore rock ledge.

Seismic profiles show the presence of a discontinuous ~27-m-deep Pleistocene trough behind the discontinuous shelf-edge reef. Where present, the trough along much of the >200-km-long margin has been filled with

landward-transported, storm-derived Holocene sand and reef rubble that, in scattered locations, is topped by skeletal Holocene reefs. Most surface traces of the trough have been obliterated, and infilling has forced progradation of those isolated parts of the shelf surface seaward. Infilling and progradational processes were rapid relative

to geologic time, having taken place only within the most recent ~7-kyr interval of Holocene flooding. Similar progradational evolution is not possible at classic, steeply inclined windward margins. Precipitous (e.g., volcanic) slopes can only aggrade seaward slowly through coral growth.

A nearshore rock ledge ~2.5 km wide cuts into the seaward side of every 125-ka Florida Keys island (Figure 6a and b). Its composition varies depending on northeast (coral) or southwest (oolite) location. Its seaward edge is ~4 m deep. Its landward edge is the shoreline. By definition, an erosional surface cannot be dated. However, correlation of physical ledge characteristics with known post-125-ka Pleistocene sea-level maxima in Florida and a local Holocene sea-level curve provide the only possible explanation as to how and when it formed. The ledge is erosional and formed during the Holocene transgression (Lidz et al., 2006).

### Other aspects

Due to space limitations, other aspects of Florida Keys reefs are not reviewed here. They include coral ecology (Jaap, 1984); effects of sewage-disposal practices (Shinn et al., 1994); diseases (Gladfelter, 1982); biochemical/physical processes, and hydrology/groundwater flow (Porter and Porter, 2002); sediment constituents (Ginsburg, 1956); and reef management (Causey, 2002).

### Summary

The late Quaternary depositional system along the shallow Florida Keys shelf was physically and biologically predisposed to replicate the structures, forms, and processes of antecedent outer-shelf and shelf-edge morphologies. Primary controls were the position of sea-level maxima relative to antecedent topography. Reefs responded to the resultant ambient geomorphic settings in their growth habits, vitality, and distribution. Post-125-ka Pleistocene settings offered accommodation space and protection, and shelf-edge reefs flourished. The Holocene transgression flooded the shelf, ultimately creating conditions that allowed tidal exchange of coastal bay and cold gulf waters with the reefs, causing their decline. The rock record shows that reef growth varied locally through time—in location, dimension, structure, geometry, depth, age distribution, and accretionary direction. Yet the recurring regional theme is the replication of antecedent facies and geomorphic landforms, and thus repetition of stratigraphic shelf-edge asymmetry. Florida Keys reef morphologies are distinctly different from what would be generated at a classic steeply inclined windward margin.

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## Cross-references

[Accommodation Space](#)  
[Acropora](#)  
[Airborne Dust Impacts](#)  
[Back-Stepping](#)  
[Calcrete/Caliche](#)  
[Holocene Reefs: Thickness and Characteristics](#)  
[Last Glacial Lowstand and Shelf Exposure](#)  
[Ocean Acidification, Effects on Calcification](#)  
[Patch Reefs: Lidar Morphometric Analysis](#)  
[Porosity Variability In Limestone Sequences](#)  
[Sea Level Change and Its Effect on Reef Growth](#)  
[Sea-level Indicators](#)  
[Spurs and Grooves](#)

## FORAM INDEX

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Benthic representatives of the protistan class Foraminifera have exceptional utility as bioindicators of coastal contamination because they have short life spans and specific niches, and therefore respond quickly to environmental change; they are commonly well preserved in the sedimentary record; they are widely distributed, yet generally regarded as relatively immobile; they are diverse; they are relatively small, abundant, and easily sampled; their collection has minimal impact on environmental resources; and the most stress-tolerant representatives are often among the last eukaryotes to disappear completely from heavily contaminated sites (Yanko et al., 1994; Schafer, 2000). In reef environments, enrichment of nutrients and therefore of organic matter tends to increase abundance and diversity of small, heterotrophic taxa at the expense of the mixotrophic larger foraminifers that host algal endosymbionts. Hallock et al. (2003) developed the Foraminifera in Reef Assessment and Monitoring (FORAM) Index (FI) to provide a simple, non-invasive indicator of whether water quality in the environment is sufficient to support coral-reef growth or recovery. The FI is calculated from foraminiferal-assemblage data from surficial sediments and is based on observations that symbiont-bearing foraminifers and zooxanthellate, reef-building corals require similar high water quality. The FI is somewhat dependent on sediment texture, so sediments dominated by coarse sands or by very fine sands or muds do not provide meaningful data.

The FI enumerates foraminiferal taxa into functional groups, calculated as follows:

$$FI = (10 \times P_s) + (P_o) + (2 \times P_h)$$

where  $P_s = N_s/T$ ,

$$P_o = N_o/T,$$

$$P_h = N_h/T$$

$T$  = total number of specimens counted

$N_s$  = number of specimens of symbiont-bearing taxa

$N_o$  = number of specimens of stress-tolerant taxa and

$N_h$  = number of specimens of other small taxa

The FI was designed as a simple, low-cost, single-metric, preliminary assessment tool to predict if prevailing water quality is sufficient to support coral-reef growth or recovery. The numerical basis for the formula is that an assemblage of 100% other small taxa yields an  $FI = 2$ . Any addition of symbiont-bearing taxa raises the FI, any addition of stress-tolerant taxa lowers the FI from that reference value. An assemblage totally dominated by other smaller foraminifers indicates there is too much food for symbiont-bearing foraminifers to occur in any abundance

(i.e., autotrophic and heterotrophic processes predominate), but not so much (or there is sufficient circulation) that biological oxygen demand in the upper sediments does not become limiting. Where oxygen becomes limiting, stress-tolerant taxa prevail. The more nutrient poor the environment, the more prevalent the mixotrophic taxa become. Calcifying mixotrophs, especially algal symbiont-bearing foraminifers and zooxanthellate corals, also tend to be longer lived and slower growing than their autotrophic and heterotrophic competitors for space, and more sensitive to highly variable oxygen because they have such high respiratory needs at night and produce excess oxygen during the daylight. For  $FI > 4$ , symbiont-bearing taxa must make up at least 25% of the foraminiferal assemblage, providing the basis for the prediction that, if  $FI > 4$ , local water quality should support calcifying mixotrophs.



**Foraminifera, Figure 1** Reticulopodia of *Marginopora* (~1.5 cm in diameter), a reef-dwelling, porcelaneous benthic foraminifer that hosts dinoflagellate endosymbionts similar to those in scleractinian corals.

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## Cross-references

Florida Keys  
Foraminifera  
Nutrient Pollution/Eutrophication

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## FORAMINIFERA

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## Definition and introduction

Members of the Class Foraminifera are among the most abundant and most useful protists in the marine realm. Foraminifers are characterized by a protective shell (commonly called a test), which can be membranous, agglutinated, or calcareous (Sen Gupta, 2002). The shell can be a single chamber or multiple chambers that are interconnected by one or more openings called foramen (plural foramina), from which the class name is taken (<http://www.ucmp.berkeley.edu/people/jlipps/glossary.html>). Foraminifers produce networks of reticulopodia (Figure 1), which are characteristic of the Phylum Granuloreticulosa. The functions of the reticulopodia include motility, attachment, feeding, excretion, and shell construction (<http://www.bowserlab.org/foraminifera/forampage.htm>).

Foraminifers are found in virtually all marine environments. Members of the Order Globigerinida are planktic; all other extant orders are benthic, though some have planktic reproductive stages (Goldstein, 2002). Benthic species live epifaunally, epiphytically, infaunally, or attached to a substrate. A wide range of environmental factors influence where individual species can live and where their shells can accumulate. However, a substantial number of studies have shown that, given suitable physical and chemical parameters, food supply is the primary determinant of population abundances of benthic foraminifers (Loubere and Fariduddin, 2002). Food supply, both quality and quantity, not only provides the energy and raw materials for individual and population growth, but also influences chemical parameters such as dissolved oxygen concentration, pH, alkalinity, and sulfide content at the sediment–water interface and within the sediments (Jorissen, 2002). In settings with excess organic matter (eutrophic environments), respiration reduces oxygen levels so that pore waters become anoxic and sulfidic, limiting habitat depth and foraminiferal abundance in the sediment. In food-limited (oligotrophic) settings, both abundance and depth distributions within sediment are limited by food supply. Intermediate food resources result in expanded gradients in food supply, pH and Eh, supporting more diverse assemblages of epifaunal, shallow-infaunal and deep-infaunal benthic foraminiferal species as compared to either eutrophic or oligotrophic environments.

The shells of individual species and assemblages have exceptional utility as environmental, paleoenvironmental and biostratigraphic indicators in marine environments and sedimentary rocks that originated in marine environments. Features that contribute to that utility include their relatively short life spans and specific niches, and thus relatively rapid responses to environmental change (Hallock

et al., 2003). Foraminiferal shells are commonly well preserved in the sedimentary record; they are diverse, relatively small, abundant and easily sampled, and their collection has minimal impact on environmental resources (Hallock et al., 2003).

While most Foraminifera are microscopic, adults of some taxa can be several centimeters in diameter (Sen Gupta, 2002). Life spans are proportional to size, ranging from days in small taxa to a few years in very large ones. The common life cycle in benthic foraminifera involves alternation of a sexual generation with one or more asexual generations (Goldstein, 2002; <http://www.ucl.ac.uk/GeolSci/micropal/foram.html>). The most common mode of asexual reproduction is multiple fission, which can produce broods of tens to hundreds or even thousands of juveniles, depending upon the volume of the parent cell. Because meiosis can precede asexual reproduction, the broods are not necessarily clones.

As early as the seventeenth century, observers of natural history began noticing the shells and fossils of the Foraminifera (Sen Gupta, 2002). Antoine van Leeuwenhoek and Carl von Linné were among the historic figures who described the complexity of what they assumed were tiny mollusks. In 1835, Dujardin concluded that foraminifera were unicellular. Despite observations of life cycles by Joseph Lister in the late nineteenth century, far fewer scientists have focused on biological studies of foraminifera than on fossil successions, distributions of shells in sediments, and shell geochemistry. Estimates of extant species range from 3,000 to 5,000, and more than 50,000 fossil species have been described (Pawlowski and Holzmann, 2008). Yet life cycles of fewer than 30 species are well documented (Goldstein, 2002). Biological research, including genetic investigations with the potential to revolutionize foraminiferal systematics, is being conducted in only a small number of laboratories worldwide.

Historically, the major groups of foraminifera have been distinguished by wall structure and composition of the shell, including organic-walled and agglutinated forms and those that produce calcareous shells (Sen Gupta, 2002). The calcareous taxa include porcelaneous imperforate and hyaline perforate shells structures, based upon crystalline nature and presence or absence of pores. Loeblich and Tappan (1992) recognized 16 suborders, which Sen Gupta (2002) elevated to orders based on Lee's (1990) elevation of the Order Foraminiferida to Class Foraminifera. Recent phylogenetic work supports assumptions that the porcelaneous taxa are fundamentally different from the hyaline taxa, indicating very early evolutionary divergence of these two lineages (Longet and Pawlowski, 2007).

Organic-walled and agglutinated benthic foraminifera can be found in most marine environments. However, they only dominate in environments where calcareous forms are stressed by reduced saturation of calcium carbonate such as hyposaline (Figure 2), relatively organic-rich, and high-latitude or deep-sea environments (Murray, 2006). Agglutinated taxa that secrete calcite cements are

common in more highly saturated environments, including open shelves and coral reefs.

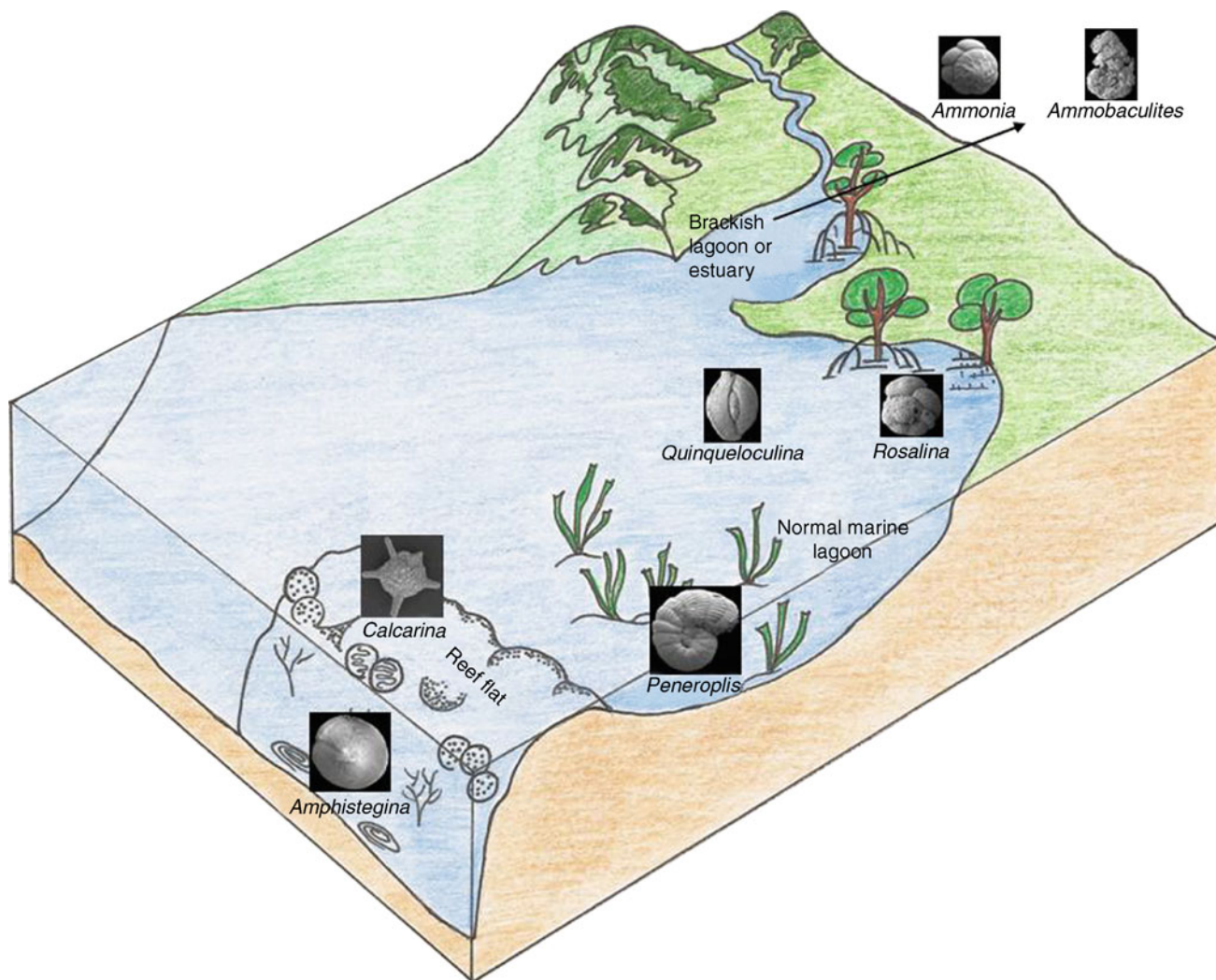
The most important foraminifera associated with environments of normal or near-normal marine salinities, including coral reefs, are those that produce calcite ( $\text{CaCO}_3$ ) shells (Murray, 2006). Many foraminiferal species use energy to exclude magnesium (Mg) ions during precipitation of calcite, resulting in shells of a few mole% of Mg. However, others, including those of the Order Miliolida that produce porcelaneous shells, precipitate their shells close to equilibrium with seawater, resulting in shells that are as much as 13–15 mole% Mg in shallow tropical waters. Calcite shells containing more than about 8 mole% Mg are relatively soluble when exposed to seawater with reduced carbonate saturation (Morse and Mackenzie, 1990). Thus, the abundance and diversity of Miliolida are good indicators of strong carbonate supersaturation. These forms will likely be among the first to decline as rising atmospheric carbon dioxide concentrations result in progressive ocean acidification (Hallock, 2000).

The other dominant benthic foraminiferal orders that produce calcite shells are the Rotaliida and the Buliminida (Sen Gupta, 2002). However, molecular phylogenetic evidence is emerging that this morphological division will require substantial revision (Longet and Pawlowski, 2007; Schweizer et al., 2008). The Rotaliida include not only some of the most stress-tolerant generalists, but also some of the most highly specialized species found among the Foraminifera (Figure 2). For example, members of the genus *Ammonia* are often the last eukaryotes to disappear from hypoxic or highly polluted habitats (Schafer, 2000). In contrast, Rotaliida that host algal endosymbionts thrive and produce vast volumes of carbonate sediments in extremely nutrient-deficient environments, yet are typically among the first species to decline under anthropogenic pollution (Hallock et al., 2003).

The majority of benthic foraminifera are heterotrophic, feeding on bacteria, algae, detritus, or combinations thereof. Feeding strategies include grazers, detritivores, suspension feeders, herbivores, and carnivores. Some Rotaliida are kleptoplastic grazers, that is, they can utilize the photosynthetic production from chloroplasts that they harvest from algae upon which they feed (Goldstein, 2002).

Several families of Miliolida and Rotaliida have co-evolved with marine algae, diversifying and morphologically specializing to the benefit of their symbiotic relationships (Hallock, 2002; Lee, 2006). The ability of a holobiont (i.e., host with algal symbionts) to both feed and photosynthesize is known as mixotrophic nutrition. This strategy is particularly advantageous in environments where both dissolved nutrients and particulate food are relatively scarce, but energy from sunlight is consistently available, even at quite reduced intensities (Hallock, 2000). Under these conditions, algal symbionts actively photosynthesize, but because they are severely nutrient limited, they excrete most of their photosynthetic products to the host. The host is thereby provided abundant energy





**Foraminifera, Figure 2** Cartoon of some habitats of benthic foraminifera. *Amphistegina* and *Calcarina* are hyaline foraminifera that host diatom endosymbionts; *Peneroplis* is a porcelaneous genus that hosts red algae; *Quinqueloculina* (porcelaneous) and *Rosalina* (hyaline) are small, heterotrophic foraminifera that are abundant in tropical coastal environments with intermediate nutrient input, while *Ammonia* (hyaline) and *Ammobaculites* (agglutinated) are heterotrophic foraminifera that can tolerate strong fluctuations in salinity, oxygen, and other chemical stresses (Drawn by Heidi Souder).

resources for metabolism and carbon-intensive processes such as mucus secretion, shell-matrix production, and lipids needed for reproduction. The few food particles the host can capture can primarily be used for the host's growth and reproduction, with only limited amount of nitrogenous wastes being released to the algal symbionts. Thus, a mixotrophic holobiont has access to literally orders of magnitude more fixed carbon than purely heterotrophic organisms in the same environment (Hallock, 1981).

Thanks to the tremendous energetic advantage of algal symbiosis, lineages of highly specialized foraminifera have evolved in mid to low-latitude reef, shelf, and bank environments several times in geologic history (Beavington-Penney and Racey, 2004). The shells of such foraminifera have been important producers of carbonate

sediments over the past 50 million years, typically associated with coralline red algae, and often with calcareous green algae and scleractinian corals or bryozoans (Pomar and Hallock, 2008). The most famous foraminiferal accumulations are the Eocene Nummulitic Limestones of Egypt, from which the pyramids were built. Similar limestones are present worldwide, where they include major aquifers and hydrocarbon reservoirs.

The algal symbiont-bearing foraminifera are often referred to as larger benthic foraminifera because many species, both extinct and extant, attained exceptionally large adult sizes, in a few cases exceeding 10 cm in maximum diameter (Hallock, 2002). Growth and calcification of substantial-sized shells over periods of months to years can only be sustained by relatively predictable

environments in which adolescent and adult mortality are low and access to sunlight is predictable (Hallock, 1985). However, extreme specialization results in high potential for extinction when environmental conditions change (Hallock, 1987). Larger foraminiferal lineages, like other major calcifying organisms, have diversified and suffered extensive extinctions numerous times in Earth history (Beavington-Penney and Racey, 2004).

A remarkable range of algae have been documented living symbiotically in members of modern families of Miliolida (Lee, 2006). The superfamily Soritacea includes one clade that hosts a rich diversity of dinoflagellate symbionts (Figure 1) similar to zooxanthellae found in reef-building corals (Pochon et al., 2007). A second clade hosts chlorophyte (green algae) endosymbionts, while a third hosts rhodophytes (red algae) (Figure 3). A separate lineage, the fusiform Alveolinidae, host diatom endosymbionts.

Diatoms are the predominant algal symbionts hosted by the Rotaliida families, including Amphisteginidae, Asterigerinidae, Calcarinidae, and Nummulitidae (Lee, 2006). *Asterigerina* are relatively small and morphologically simple, while members of the Nummulitidae have highly specialized internal structures to accommodate not only the symbionts, but also light-gathering and cytoplasmic exchange among chambers and with the environment (Hottinger, 2000, 2006). Individuals of the nummulitid species, *Cyclocypeus carpanteri* (Figure 4) are among the largest foraminifera known, either extant or fossil, with diameters of 6 cm common (Hohenegger et al., 1999).

Foraminifera occur abundantly on coral reefs and associated environments such as reef flats, lagoons, reef slopes, and oceanic banks (Murray, 2006). The Miliolida are particularly diverse, because warm, normal salinity to

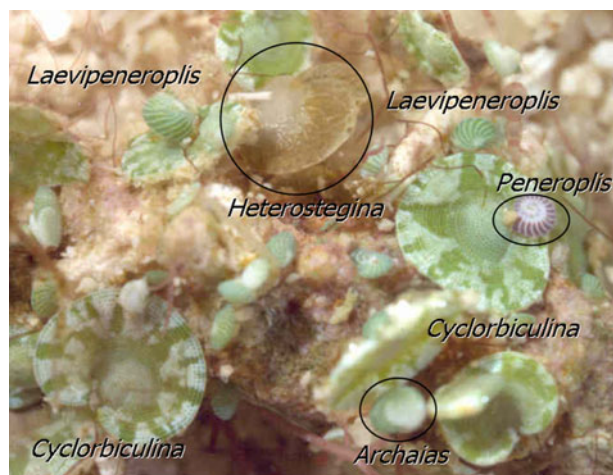
slightly hypersaline seawaters are typically highly supersaturated with respect to calcium carbonate, which enhances rates of precipitation of their Mg-calcite, porcelainous shells. Symbiont-bearing Miliolida tend to be most abundant in waters less than 30 m deep (Hohenegger et al., 1999; Hallock, 2002). In the Indo-Pacific, large coin-shaped *Marginopora* (Figure 1) and *Amphisorus*, which harbor zooxanthellae, can be conspicuous in reef flat environments. Western Atlantic and Caribbean reef flats and lagoons are populated by green algae-bearing *Archaias* and *Cyclorbiculina* (Figure 3), which can be extremely abundant on seagrass, macroalgae, and reef rubble.

Rotaliida more often dominate reef assemblages, though species diversity is typically less than for the Miliolida. Smaller heterotrophic taxa, including kleptoplastic species, are common and sometimes abundant. But, relative to foraminifera, modern reef margins and slopes are the domain of the symbiont-bearing Rotaliida. The ubiquitous *Amphistegina lessonii* and *A. lobifera* in the Indo Pacific, and the Atlantic counterpart *A. gibbosa*, often totally dominate foraminiferal assemblages. Where the Calcarinidae (Figure 5) thrive in the Indo-Malay region, they can totally overwhelm even *Amphistegina* (Hohenegger, 2006). In Okinawa, small bottles of beautiful “star sands” are even sold in souvenir shops. Representatives of the Nummulitidae are most common at depths of 30–100 m or more (Hohenegger et al., 1999).

The larger foraminifera in the Indo-Pacific exhibit strong depth zonation (Hohenegger et al., 1999; Renema, 2005), with robust morphologies abundant at less than 10 m depth and increasingly flatter species occurring down to the extreme limits of sufficient light penetration for photosynthesis (Figure 6). Like stony corals, flatter, thinner morphologies are more advantageous as light diminishes with depth.

Biological and ecological studies of foraminifera with algal endosymbionts began in the 1960s, primarily to improve paleoenvironmental interpretations of foraminiferal limestones. As some coral reefs began to exhibit stress and coral cover began to decline in the 1970s and 1980s, abundances of larger foraminifera were observed to trend similarly to coral cover (Cockey et al., 1996). Then, in 1991–1992, *Amphistegina* populations in both the western Atlantic-Caribbean and Indo-Pacific were observed bleaching, providing further evidence that environmental causes of reef decline were also impacting these protists (Hallock, 2000).

Foraminiferal assemblages, especially the abundance and diversity of symbiont-bearing taxa, hold much potential as indicators of water quality decline that can reduce the advantage of mixotrophic nutrition (Hallock et al., 2003). However, the differences in trophic roles of different foraminiferal groups, and the differences in responses to increasing food supply, must be considered when interpreting assemblage data. Researchers often assume that the highest diversities and abundances indicate the most favorable conditions (Murray, 2006). However, in

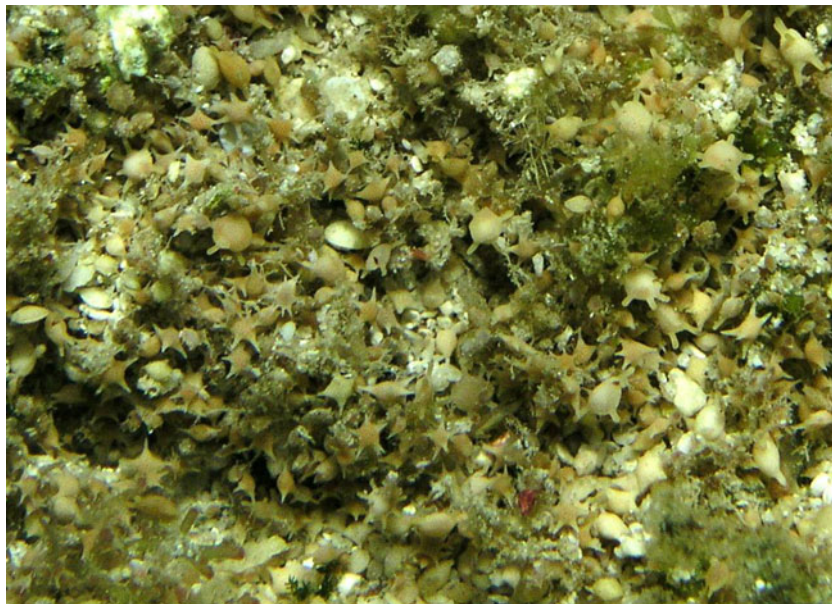


**Foraminifera, Figure 3** Larger foraminifera from the Florida Keys including *Archaias* (~1 mm in diameter), *Cyclorbiculina* and *Laevipeneroplis* that host green algae as endosymbionts, *Peneroplis* with red algae, and *Heterostegina* with diatom symbionts.





**Foraminifera, Figure 4** A live *Cycloclypeus carpenteri* (~5 cm in diameter), photographed in situ (photo by W. Renema).



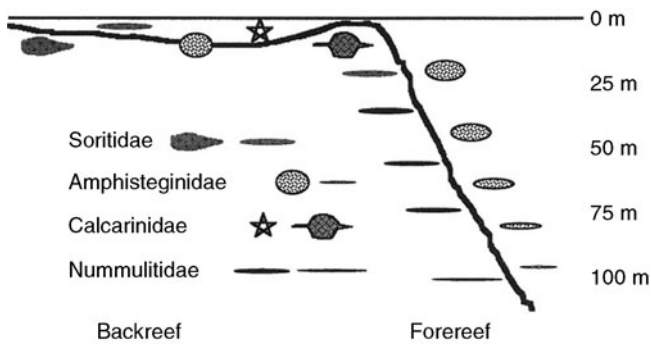
**Foraminifera, Figure 5** In situ photograph of live *Baculogypsina* and *Calcarina* (~1–3 mm in diameter) (photo by W. Renema).

warm, shallow, oligotrophic marine environments, where food supply limits abundance and diversity of heterotrophic species (and therefore overall abundance and diversity), dominance by several algal symbiont-bearing species often indicates high water quality. Higher overall foraminiferal diversity and abundance indicates higher nutrient flux, typically from terrestrial sources.

### Conclusions

Reef-dwelling foraminiferal assemblages can be used as indicators of whether water quality supports prolific calcification by symbiont-bearing organisms. However, the total influence of local, regional, and global environmental changes associated with human activities impacts symbiont-bearing taxa somewhat differently than reef-building corals. Thus,





**Foraminifera, Figure 6** Cartoon representation of shape trends with depth in four families of reef-associated larger foraminifera (adapted from Hallock, 2002).

it is important to understand when foraminiferal assemblages respond in parallel with corals and when they do not.

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## Cross-references

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## FOREREEF/REEF FRONT

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### Synonyms

Outer reef margin; Outer reef slope; Reef face; Reef slope

### Definition

The forereef is the outside part of a reef seaward of the reef crest (or reef edge) facing open sea.

### Morphology

The forereef is characterized by peculiar morphological features (Guilcher, 1988; Hopley et al., 2007). The most common feature is the inclination of the slope marked by some breaks and sometimes the occurrence of more or less flat terraces or platforms. The forereef is also characterized by the occurrence of spur and groove system in the upper parts, and sometimes by landslides or slipped blocks. Drowned reefs can be unusual morphological features observed in some forereefs. The forereef can be distributed into shallower and deeper zones.

### Factors controlling the morphology

The morphology of the forereef slopes depends on both climatic and tectonic variations and is controlled by several factors including the following (non exhaustive list): (1) the inheritance of morphology (ancient reefs formed during the past sea level variations) (2) the antecedent morphology depending on subaerial exposure and alteration (karstification) during the low stands of sea level; (3) processes of cementation; (4) biological activity taking into account the competition between the various organisms and depending on the degree of water energy and irradiance; (5) collapse and slides resulting from storms, hurricanes, seismic events, or tsunamis; (6) the bioerosion; and (7) the interaction of currents.

### Biozonation

The upper parts of the forereef slope are exposed to the strong wave energy and are characterized by the algal crest in the Indo-Pacific region and by spurs and grooves extending downward. Many boulders and various debris materials can be found. The living corals are generally abundant. In the Caribbean, six types of breaker zones (upper parts of the forereef) were defined depending on the degree of energy of wave exposure (Geister, 1977) displaying some regional variations.

The deeper parts of the forereef slope are generally poorly investigated and consequently little is known from this zone. This area can be marked by steep slope as observed in French Polynesia (Montaggioni et al., 1987) and is characterized by the low degree of water energy and irradiance. Some submersible observations were

performed along the forereef slopes as for example in Jamaica (Land and Moore, 1977) and in Belize (James and Ginsburg, 1979) in the Caribbean, and in Tahiti (Salvat et al., 1985) in the Pacific, where some morphological features were recognized as submerged terraces or series of steps or blocks falling from the above modern coral reefs.

### Biological encrusting zonation

A recent study performed in New Caledonia (Flamand et al., 2008) revealed the occurrence of several biofacies along the forereef comprising mainly bindstones dominated by coralline algal and/or foraminiferal crusts. Based on these observations and taking into account the distribution and abundance of the coralline algae and acervulinid foraminifera depending on the degree of water energy and irradiance, a model of bathymetric range of encrusting organisms was proposed. The coralline algae rich in mastophorids and/or lithophylloids are abundant in the upper parts of the forereef, the coralline algal assemblage rich in melobesoids, *Sporolithon* sp., and *Peyssonnelia* sp. in the deeper parts, and foraminiferal crusts are dominant below 90 m progressively replacing the coralline algal crusts.

### Occurrence of micritic crusts

Laminar micritic crusts were observed in the Red Sea by Brachert and Dullo (1991) on the ledge-rocks from 120 to 200 m. Such crusts were also observed on the forereefs from Belize and Jamaica (James and Ginsburg, 1979; Land and Moore, 1980). In Tahiti, in French Polynesia, relatively thick crusts recovered from 80 to 130 m were interpreted as microbialite crusts (Camoin et al., 2006).

### Summary

The morphology of forereefs mainly reflects the effects of reef growth in interaction with the sea level variations and in combination with the subsidence and uplift movements. Little is known regarding the distribution and the abundance of organisms especially in the deeper parts. Nevertheless, the biological assemblages appear to be distributed characteristically with the water depth depending on the degree of wave energy and irradiance.

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## Cross-references

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## FOSSIL CORALLINE ALGAE

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### Definition

Fossil coralline algae are the remains in the geological record of a group of calcified marine red algae (Corallinales, Rhodophyta), which are common components in coral reef environments and can be significant framework builders.

### Introduction

Coralline algae are the major extant group of calcareous red algae. As a group, they are cosmopolitan and have wide ecological tolerances. They are common on seafloors with low terrigenous supply at depths of up to 100–120 m in all climatic belts. Individual species and genera, however,

have restricted dispersal areas and sensitivity to light conditions, trophic levels, wave energy, salinity, and other ecological factors, all of which limit their geographic and environmental ranges.

The body (thallus) of corallines consists of filaments of cells joined together to form a coherent mass. Most extant coralline algae are pervasively calcified by high magnesian calcite precipitated in the cell walls. In crustose coralline algae (CCA), also known as non-geniculate corallines, all vegetative cells except those at the thallus surface are calcified. Consequently, the entire plant is rigid, with varying degrees of fragility, and a high preservation potential as fossils (Bosence, 1991).

In contrast, in geniculate (articulated) corallines, calcified segments of the thallus are separated by noncalcified joints (genicula). Articulated corallines have bushy thalli formed by branches for which the joints offer flexibility. After death, articulated corallines disintegrate and calcified segments are shed as sand and gravel particles.

CCA are common components in coral reef environments and can be major framework builders in algal ridges (Adey, 1986). Accordingly, CCA are significant components in fossil coral reefs (Figure 1). Like their living counterparts, fossil CCA can occur attached to hard substrates, typically coral skeletons, cemented reef rock, shells, and other calcified algae. CCA can also be unattached, occurring as nodules generally termed rhodoliths or as loose branching growths within gravel or sand deposits. Fragments of CCA and calcified segments of geniculate corallines are abundant in reef debris and carbonate packstones and grainstones associated with fossil reefs.

Diagnostic features for delimiting families and subfamilies and many diagnostic characters used to separate genera and species can be recognized in fossil plants in ultrathin sections (less than 20 microns) with an optical microscope (Figure 2) and scanning electron microscope (SEM) after light etching (Braga et al., 1993). In some cases, however, the diagnostic characters to distinguish genera and species in living corallines correspond to uncalcified reproductive structures that are not preserved or are difficult to discern in fossil corallines. Fossil plants of the majority of the main CCA species of modern reefs usually preserve characters that permit their identification. In a few cases, the preserved anatomic features only warrant the identification of a species group within a genus. A species group is a set of species that share a series of characters separating them from other species of the genus. Plants with very thin laminar thalli (less than 0.02 mm in thickness) are commonly micronized and usually cannot be identified. Therefore, they are not taken into account in palaeoenvironmental interpretations based on fossil CCA.

### Applications of fossil CCA

The habitat preferences of different genera and species, the variations in morphology according to turbulence





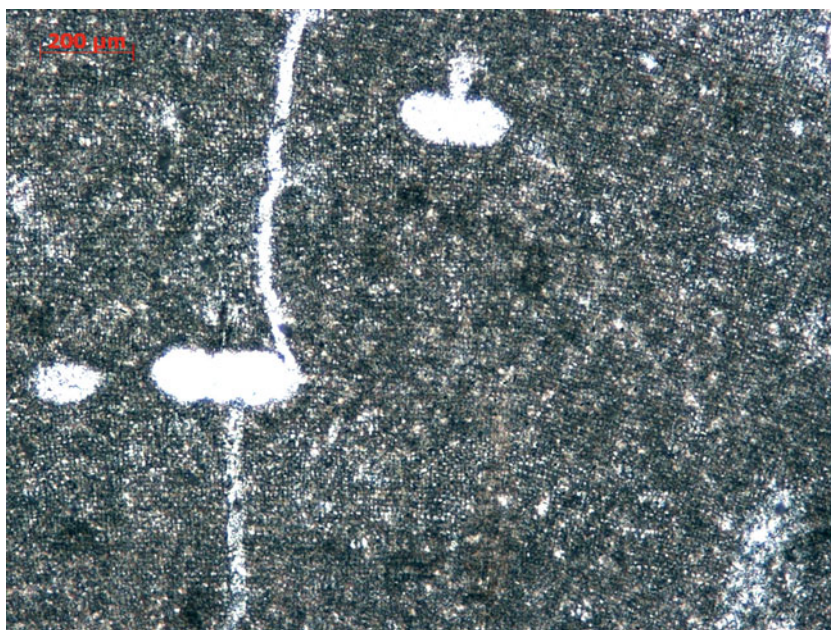
**Fossil Coralline Algae, Figure 1** Last deglacial reef framework in Tahiti. Coralline algae (white) encrusting branching corals (beige) and overgrown by a laminar coral (beige, top right). Crustose coralline algae (CCA) are intensely bored by sponges.

levels, and their high preservation potential make fossil CCA very useful palaeoenvironmental indicators (Adey, 1986). Light is the primary factor controlling the distribution of CCA species and, as light intensity and wavelength reaching the seafloor strongly depends on depth, CCA species have limited depth ranges. The ranges of CCA genera are less defined, but some genera show distinctive depth zonation. CCA genera and several of their species living in coral reefs have a pantropical distribution. Other species are held to be “paired,” occurring as vicariant species, playing similar ecological roles, in the Caribbean and in the Indo-Pacific. In cases where taxonomic revisions have been undertaken, they have shown that species pairs are actually heterotypic synonyms.

CCA taxa have a slow rate of morphological evolution and high longevity (Bosence, 1991). As result of this trait, the immense majority of coralline taxa identified in Quaternary reefs are living today and their present-day environmental distribution can be used to interpret the palaeoenvironments in which they lived. In particular, depth ranges of living CCA can be applied to discern the palaeobathymetry of the deposits in which fossil CCA occur.

Assuming that CCA species, species groups, or genera are correctly identified, certain other aspects might limit the validity of this “transferred ecology” approach. First, any postmortem displacement of fossil plants from their original habitat has to be discarded. CCA encrusting corals in reef frameworks offer the most positive proof of in situ preservation. In contrast, taphonomic and sedimentological observations are needed to convincingly assume the absence of transport of rhodoliths or algal fragments occurring in gravels and sands. Second, the understanding of the ecology of present-day corallines is uneven and limited for many areas. The depth distribution of CCA is relatively well known only from a certain number of regions through field guides and monographic papers. The reported depth ranges are patently affected by sampling depth and probably by the area surveyed, and therefore the data for a single taxon from different regions are not always coincident. In addition to biases introduced by surveying procedures, factors influencing light penetration (such as turbidity) can also affect the depth distribution of CCA species. Even though the majority of genera and many species in living reefs probably have broadly similar ecological requirements across the oceans, their depth ranges may vary between areas. Ideally, the palaeoenvironmental interpretation of fossil corallines in a Quaternary reef should be based on the ecological distribution demonstrated by the species living in the same area. Third, some taxa may change their environmental requirements over time, although this factor is probably negligible for late Quaternary reefs.

Summarizing available data on the environmental distribution of modern CCA from the last few decades (Adey et al., 1982; Adey, 1986; Verheij and Erftemeijer, 1993; Iryu et al., 1995; Cabioch et al., 1999; Littler and Littler, 2000, 2003), three distinct zones can be defined by



**Fossil Coralline Algae, Figure 2** Microphotograph of Pleistocene *Hydrolithon onkodes* in thin section.

the depth ranges of genera and species (Figure 3). This zonation follows the one proposed by Webster et al. (2009) for reef facies in Quaternary Pacific reefs. The main components of these zones and their characteristic growth forms, together with the resulting carbonate facies, are summarized below.

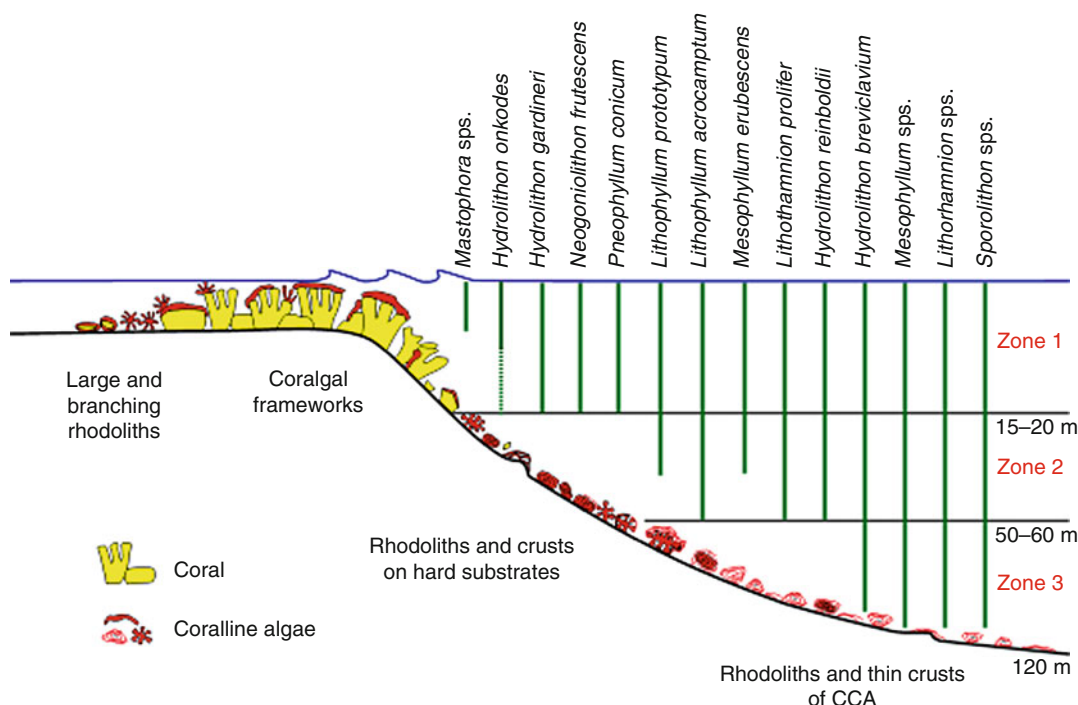
**Zone 1.** Shallow coral reef (0 m to 15–20 m). This zone is dominated by coralline frameworks in which CCA encrust massive and branching corals and intergrow with encrusting corals and other sessile organisms. In the Indo-Pacific, centimeter-thick plants of *Hydrolithon onkodes* dominate the algal assemblages at less than 10 m (Figures 1 and 2). Thin crusts of *H. onkodes* and several species belonging to the subfamily Mastophoroideae, such as *Hydrolithon gardineri*, *Hydrolithon munitum*, *Hydrolithon reinboldii*, *Neogoniolithon fosliei*, *Neogoniolithon frutescens*, *Pneophyllum conicum*, and *Spongites yendoi* are also common throughout this shallow-water zone. Large rhodoliths formed by plants of these species occur in back-reef areas and lagoons. Branching plants of the *Lithophyllum kotschyannum* species group occur attached to the reef framework or forming rhodoliths in the lagoon gravels and sands. In the Caribbean, *Hydrolithon pachydermum* plays the role of *H. onkodes* in the Indo-Pacific. *Lithophyllum congestum* occurs in reef crests and other *Lithophyllum* species extend to deeper settings. Branching growths of *Neogoniolithon strictum* form open frameworks and rhodoliths in back-reef areas and lagoons. CCA that are typical of deeper zones (such as *Lithothamnion*, *Mesophyllum*, *Lithoporella*, and *Sporolithon* species) can overgrow

the shallower-water species mentioned in the paragraph above or encrust the same coral colony on a different side. This occurs since light controls coralline distribution, and therefore shade habitats in the framework, such as crevices, caves, and cavities, are dominated by the same CCA as those living in open deep environments. Similarly, shallow-water species can be overgrown by shade species when the framework substrate in which they grew becomes overshadowed by new coral growth. In fossil reefs, this zone is represented by in situ coralline frameworks (framestones, bindstones, and bafflestones) or CCA crusts on large coral fragments.

**Zone 2.** Intermediate fore-reef slope (15–20 m to 50–60 m). CCA occur as rhodoliths in gravels and sands in the reef slope or as crusts on hard substrates (minor corals, lithified reef deposits). Rhodoliths are typically formed by thick fruticose and warty layers of CCA. In the Indo-Pacific, *Mesophyllum erubescens* and *Lithophyllum prototypum* (also reported as *Titanoderma tessellatum*) are typical of the shallower part of this zone. *Hydrolithon reinboldii*, *Lithothamnion prolifer*, and *Lithophyllum acrocamptum* are common down to 40–50 m. *Mesophyllum erubescens* and *Lithophyllum prototypum* also occur in this zone in the Caribbean, together with *Hydrolithon boergesenii*, *Neogoniolithon* species, and *Lithothamnion ruptile*. In fossil reefs, this zone is characterized by rhodolith floatstones and rudstones and CCA bindstones with encrusting foraminifers and with minor corals.

**Zone 3.** Deep fore-reef slope (50–60 m to 120 m). The lower limit of CCA distribution is usually around 120 m, but thin plants can grow on much deeper settings





**Fossil Coralline Algae, Figure 3** Depth ranges of common CCA in the Indo-Pacific reefs. Depth zonation of an idealized back reef/reef slope transect, which can be applied to interpret palaeodepth in fossil reefs.

(down to 270 m, Littler et al., 1985). CCA occur as nodules in carbonate sands or as thin crusts on hard substrates frequently intergrown with encrusting foraminifers, forming complex, multigenerational open frameworks. The genera *Lithothamnion* and *Mesophyllum*, belonging to the subfamily Melobesioideae, dominate the algal assemblages together with *Sporolithon* and the red alga *Peyssonnelia* both in the Indo-Pacific and the western Atlantic. *Lithoporella* is also common in this zone in the Indian and Pacific oceans. In fossil reefs, this zone is represented by rhodolith floatstones and rudstones, and coralline algal and foraminiferal crust-dominated bindstones, with the above-mentioned algae.

This zonation model can be applied to interpret the palaeobathymetry of fossil CCA and the reef deposits in which they are found. Since deeper-assemblage species may occur with those characteristic of shallower depths, the zone is identified by the maximum depth range of the shallowest CCA present.

The relative abundance of CCA is indicative of water turbidity as the CCA cover in modern reefs is higher in clear waters with no terrigenous influx (Fabricius and De'ath, 2001). Species richness is probably correlated to water clarity as well.

## Summary

Coralline algae, particularly the crustose species (CCA) are common components in fossil coral reefs. CCA

possess a calcitic skeleton with a high fossilization potential.

Fossil CCA occur attached to hard substrates or unattached, as nodules or as loose branching growths and fragments within gravel or sand deposits. The majority of CCA species identified in Quaternary reefs all over the world are living today and their present-day habitat preferences can be used to interpret the palaeoenvironments in which they lived, especially palaeodepth. Three depth zones can be distinguished according to available data on the depth ranges of modern CCA. These zones can be applied to infer palaeobathymetry in Pleistocene and possibly older reefs. Zone 1, in the shallow coral reef (0 m to 15–20 m) is characterized by thick CCA crusts on corals. Thick plants of *Hydrolithon* and other species of the subfamily Mastophoroideae and branching plants of *Lithophyllum* are common throughout this shallow-water zone. Large rhodoliths formed by these species occur in back-reef areas and lagoons. In Zone 2, in the intermediate fore-reef slope (15–20 m to 50–60 m), CCA occur as nodules in gravels and sands in the reef slope or as crusts on hard substrates. Several species of *Mesophyllum*, *Lithothamnion*, *Lithophyllum*, and *Hydrolithon* appear in this zone. The melobesioids *Lithothamnion* and *Mesophyllum*, together with *Sporolithon* and the red alga *Peyssonnelia* are typical of Zone 3 (50–60 m to 120 m or more). In this deeper fore-reef slope, CCA occur as nodules in fine reef debris or as thin crusts, commonly intergrown with encrusting foraminifers on hard substrates.



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## Cross-references

Algae, Coralline  
 Binding Organisms  
 Emerged Reefs  
 Packstone  
 Rhodoliths  
 Submerged Reefs

## FRAMESTONE

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Framestone is a modification proposed by Embry and Klován (1971) to the Dunham (1962) Boundstone type

of limestone where the framework organisms provided a rigid framework.

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## FRINGING REEF CIRCULATION

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## Synonyms

Fringing reef hydrodynamics

## Definition

Fringing reef circulation is the flow of water generated by wave, tide, and wind generated currents, over and adjacent to fringing reefs and in their associated lagoons, including flow patterns resulting from water movements interacting with elements of the reef morphology.

## Introduction

Fringing reefs have been described as being morphologically simple (Kennedy and Woodroffe, 2002), but variation in important parameters such as the reef morphology, tidal range, and wave energy means that a widely applicable model of fringing reef water circulation does not exist. Fundamental distinctions can be made between fringing reefs with or without an enclosed lagoon, those on the windward shores (with circulation normally driven by waves) or leeward shores (with tidal and other currents dominating), and those enclosed by headlands (where topographically controlled circulation is important) or those that extend along a more or less straight shoreline. Other reef types that could be described as fringing are variously described as either fringing or barrier (e.g., Ningaloo Reef, Australia; Hearn, 1999), bank-fringing (e.g., Great Pond Bay, St Croix, U.S. Virgin Islands; Lugo-Fernandez et al., 1998b), bank-barrier (e.g., Tague Reef, St Croix; Lugo-Fernandez et al., 2004), or coral lagoons (e.g., Kaneohe Bay, Oahu, Hawaii; Hearn, 1999). Other authors have described reefs adjacent to coral cays as fringing (Daly and Brander, 2006).

## Waves and wave generated circulation

Wave driven circulation on coral reefs has received considerable attention, with many processes on both fringing and non-fringing reefs being generally similar. When waves reach a reef, shoaling is rapid and the surf zone is narrow, with most energy expended over a short distance at the reef edge or at the reef crest. Most energy (60–97%) is lost during the wave shoaling, breaking, and reforming processes (Gourlay, 1994; Lugo-Fernandez

et al., 1994; Daly and Brander, 2006), with energy dissipation due to bottom friction contributing significantly to, and perhaps dominating, the overall energy reduction (Lugo-Fernandez et al., 1998a; Lowe et al., 2005). A relatively small proportion of the wave energy reaches the back reef or lagoon. Tidal range is an important controlling factor (Hardy et al., 1991a, b) because of its influence on the water depth over the reef crest. At low tide, little or no wave energy crosses the reef flat. At mid tide, most waves break, energy is dissipated, and some waves re-form as bores, passing over the reef flat as solitary waves and reforming (if a lagoon is present). At high tide, waves may break and reform, or under low energy conditions or in situations with a high tidal range, waves may pass over the reef crest onto the reef flat or into the lagoon, and travel to the beach with little loss of energy. Lugo-Fernandez et al. (1998b) reported an average 62% wave attenuation between the fore-reef and the reef crest and 90% attenuation between the fore-reef and the back-reef lagoon, in the low tidal range environment of St Croix., with wave attenuation being significantly higher at low tide. Following breaking, a broadening of the wave spectrum occurs (Young, 1989; Hardy and Young, 1991). A maximum for the wave limiting parameter (wave height/mean water depth) of about 0.55 as reported by Gourlay (1994), Nelson (1994), and Kench and Brander (2006) is applicable to fringing reefs.

Some studies have demonstrated that infragravity waves, perhaps generated by shelf resonance, can be significant (Roberts and Suhayda, 1983), although their overall importance remains unclear (Lugo-Fernandez et al., 1998c). Low frequency resonance is also described by Peguignet et al. (2009), who hypothesize that during high energy events, resonance leads to a significant increase in wave energy reaching the shoreline.

Wave setup is of prime importance in driving water across the reef crest into the lagoon or onto the reef flat on fringing reefs. Lowe et al. (2009) found wave setup to be roughly proportional to offshore wave energy flux, above a lower threshold where setup was minimal. Jago et al. (2007), in a study on the (non-fringing) Lady Elliot Island (Great Barrier Reef) reef, demonstrated secondary wave setup on the beach, a factor not incorporated into previous models. The effects of setup on reef water circulation is described by Gourlay (1996a, b) and Gourlay and Colleter (2005). Symonds et al. (1995) showed reef and lagoonal currents were proportional to off-reef wave height after tidal effects had been removed. Hearn (1999) introduced the concept of current depth coefficients on the basis of studies in Kaneohe Bay and on Ningaloo Reef, predicting a linear relationship between the height of incoming waves and the speed of the current across the reef and through the lagoon. However, although modeling studies of wave setup on reefs now abound, field verification remains limited, and important assumptions have not been tested. Importantly, Hearn (1999) points out that variable wave friction which is dependent on depth means that the hydrodynamics of fringing reef

systems is highly non-linear, and this is a severe restriction for laboratory or modeling studies.

Many studies emphasize the importance of channels for water returning to the open sea (e.g., Roberts et al., 1975; Roberts, 1981; Marsh et al., 1981; Yamano et al., 1998; Lugo-Fernandez et al., 2004). Setup generated flow drives water into the lagoon (where one exists), and balance is maintained by preferential return flow through channels (Lowe et al., 2009), a process analogous to rip formation on beaches (Roberts, 1981). Longshore currents develop to carry water to the channels. Velocities in channels up to  $1.5 \text{ ms}^{-1}$  are reported by Coronado et al. (2007), with maximum currents within the lagoon being  $0.6 \text{ ms}^{-1}$ , which is in the same order as reported by other studies (e.g., Marsh et al., 1981). Tamura et al. (2007) show that although flows towards channels are expected to dominate when wave-generated flow into the lagoon is significant, the same circulation pattern exists even when wave energy is small, despite the presence of tidal currents. Jago et al. (2007) note that it is generally assumed that a return to the mean water level landward of the reef to the open ocean water level takes place by flows through a lagoon. In cases where a lagoon does not exist, as is the case on many fringing reefs, it is suggested that alongshore variation in wave setup drives along reef flows which have the same function as cross-reef directed flows through lagoon openings.

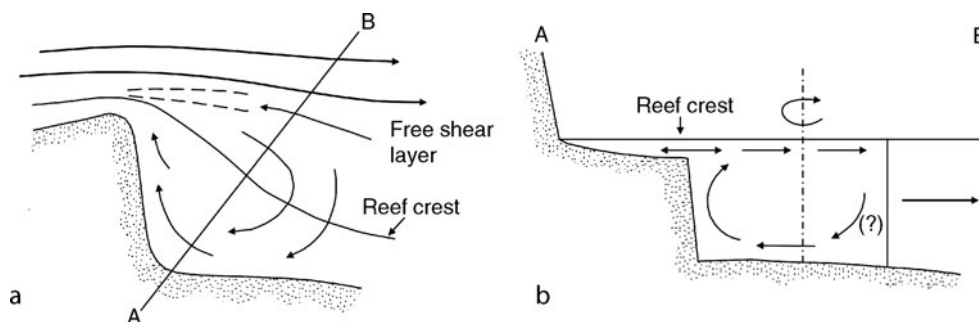
### Wind-generated circulation

When wave energy is low, circulation can be dominated by flows generated by trade-winds. Roberts (1981) reports that currents of  $0.5\text{--}0.8 \text{ ms}^{-1}$  for durations of 2–6 s are common under such conditions, although typical wind generated flows are in the range of  $0.10\text{--}0.25 \text{ ms}^{-1}$ . Presto et al. (2006), in a study on Molokai, Hawaii, showed that trade-wind generated flows dominated circulation and sediment flux. In a study on the Puerto Morelas fringing reef system, Mexico, Coronado et al. (2007) found trade wind generated flows were small, and concluded that wind influence through wind-wave generation was the most effective wind influence. Trade-wind generated waves were also reported to increase sediment suspension by Storlazzi et al. (2004).

More generally, on wide reef flats or in wide lagoons, high-frequency wind waves can be generated, the frequency and direction of which can be quite different from those of waves that have traveled from the reef edge (Kench and Brander, 2006).

### Topographically controlled circulation

At a regional scale, circulation on fringing reef shores is dominated by larger scale circulation related to features such as shelf waves and tides, modified locally by the influence of waves (Monismith, 2007). In these cases, where fringing reefs interact with regional circulation, reefs will generate large scale three dimensional eddies, similar to those shed by any topographic feature in moving



**Fringing Reef Circulation, Figure 1** Fringing reef eddy circulation in the lee of a headland (a) plan view (b) side view (Hopley et al., 2007).

water (Wolanski, 1986). At smaller scales, wave-driven circulation might be expected to dominate on windward coasts, whereas on leeward shores, the interaction of tide-generated or wind-generated currents with the local topography will set up topographically controlled circulation patterns, with eddy circulation dominating.

Eddies were found to dominate circulation on embayed fringing reefs in the Great Barrier Reef region (Figure 1) (Parnell, 1988a, b). The radius of the eddy was dependent on the incident angle between the headland shedding the eddy and the current, the degree of indentation of the bay, and the morphology of the reef front (Hopley et al., 2007). The radius of the eddy was greatest where the incident angle was highest and the eddy was strongest where the bay was enclosed by headlands at each end, with water being deflected against the opposing shore. Eddy circulation was established quickly following the establishment of a tidal stream. Velocities within the eddy (over the reef flats) were found to be independent of tidal stream velocities and generally less than  $0.2 \text{ ms}^{-1}$ . Wolanski (1993) identified the presence of a narrow free shear layer (an area inhibiting water circulation across it) extending to the seabed and comprising numerous small eddies, in such situations. Lines indicating the shear can often be seen extending a considerable distance downstream of headlands. Eddy circulation was accompanied by upwelling of water at the reef front.

## Flushing

Water circulation is the most important driver of flushing (alternatively called turnover or residence). The parameters used to measure flushing vary widely between studies and direct comparisons are normally impossible. Flushing is strongly influenced by the presence (or absence), nature, and size of a lagoon. Residence times can vary significantly by an order of magnitude for different parts of a system, such as in Kaneohe Bay, where areas with physical separation from the ocean can have residence times of 1–2 months (Lowe et al., 2009). Some studies, for example Kraines et al. (1998), report very short (<5 h) residence times in a shallow lagoon system using calculations based on the flow field. Headland enclosed fringing reefs

with no lagoons and with well developed eddy circulation are typically very well flushed (Parnell, 1988a), with residence times of close to one tidal cycle on spring tides.

## Summary

Fringing reef circulation varies depending on a range of factors, the most significant being wave energy, the presence or absence of a lagoon, the presence of channels through the reef front, and the nature of topographically controlled circulation. Wave setup driven flow is the most important driver in windward locations, with trade-wind generated flows or tidal flows interacting with local topography being most important in leeward locations.

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## Cross-references

[Boat Channel](#)  
[Fringing Reefs](#)  
[Lagoon Circulation](#)  
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[Reef Flats](#)  
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## FRINGING REEFS

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## Definition

“Fringing reefs” are reefs that grow very close to the shore on mainland or high island (continental shelf or volcanic mid-ocean island) coasts. They are generally shore-attached, although back-reef areas can be shallowly submerged. Most fringing reefs are simple structures geomorphologically which can be divided into three main zones: forereef, reef crest, and backreef. They tend to be relatively narrow reefs where the submarine slope is steep and broader where it is gentle, and they usually consist of a thin but seaward thickening veneer of reefal carbonate deposited over a rocky substrate. Fringing reefs are the first in the subsidence-driven Darwinian reef sequence (fringing reef – barrier reef – atoll; Darwin, 1842). They are often relatively young reefs and tend to be best developed on stable or rising coasts.

## Introduction

In the 30 plus years since Steers and Stoddart (1977) suggested that

*Of the three main types, fringing reefs are the simplest, apparently the least in need of complex explanations, and also the least studied.*

There have been numerous geomorphological studies of fringing reefs, including morphostratigraphic and geochronological investigations. These studies show that although many fringing reefs are relatively thin structures of recent age, their growth and development is usually more complex than formerly recognized. Kennedy and Woodroffe (2002) provide an excellent review of geomorphological research on fringing reefs that summarizes this complexity. The proliferation of fringing reef research since the late 1970s occurred partly because they are the most common type of reef (more than 50% of the total reef area globally – Hopley, 2004), and they are relatively easy reefs to access compared to those offshore, but another significant motivation has been their perceived vulnerability to threats associated with land-based human activities (see *Nutrient Pollution/Eutrophication*). In recent years, this interest has intensified as many fringing reefs are reportedly in decline, even on the Great Barrier Reef (GBR) – the world’s best protected reef ecosystem (e.g., McCulloch et al., 2003; Fabricius, 2005; Wilkinson, 2008) (see *Great Barrier Reef: Origin, Evolution, and Modern Development*).

Following Darwin’s classification (1842) (see Darwin, Charles (1809–1882)), fringing reefs are interpreted as the first stage in a long-term evolutionary sequence, in which reef growth is initiated over a substrate on the shoreline where it simply grows upward and outward (Figure 1a), but later becomes separated from the shore as the underlying substrate gradually subsides and a leeward lagoon develops (see *Subsidence Hypothesis of Reef Development*). Fringing reefs are thus widely associated with stable or uplifting coasts, where the lack of subsidence impedes the transition from fringing to barrier reef. However, as

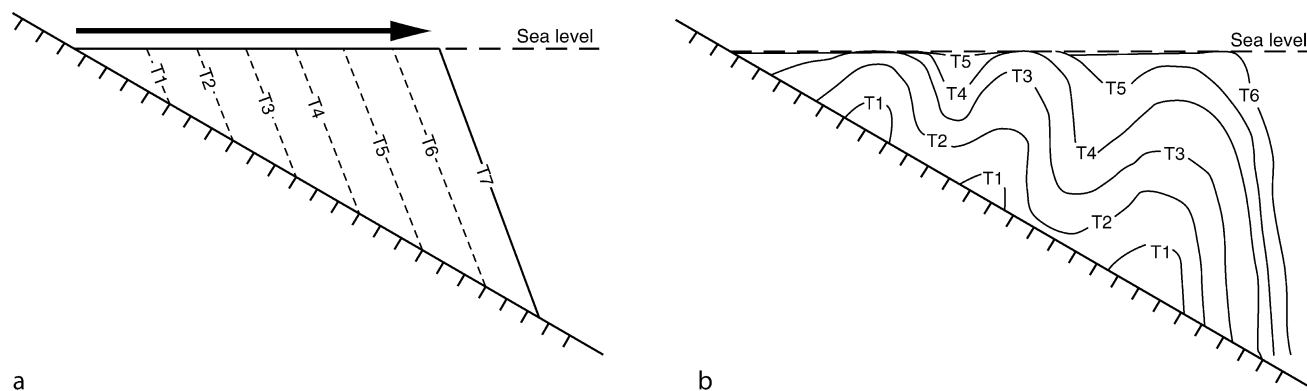
discussed later in this entry, slow geological subsidence has generally had little influence on modern fringing reef growth compared to more rapid changes in relative sea level throughout the Holocene (see *Postglacial Transgression: Sea-Level Change and Its Effects on Reef Growth*).

A water depth over the backreef of less than 10 m is usually the principal criterion used to define a reef as a fringing reef (Milliman, 1974). A narrow back-reef lagoon width has also been suggested as a trait that differentiates fringing from barrier reefs (e.g., Purdy and Winterer, 2006), but as no quantitative standards are provided, this subjective diagnostic criterion is of little value. The distinction between fringing reefs and barrier reefs can be ambiguous, with Tayama (1952) proposing a transitional class termed “almost-barrier” reefs based on his observations through Micronesia. Intermediate forms have been described at sections of the Huon Peninsula, Papua New Guinea, where the reef crest is separated from the shoreline by a depression deeper than is usual for a fringing reef (Chappell, 1974), and laterally reefs may vary from fringing to barrier in character, as is the case along the Kenyan coast (Bird and Guilcher, 1982).

Most attempts to understand fringing reef development focus on the influence of two primary controls:

1. The adjacent landmass, specifically its lithology and topography, and the delivery of freshwater runoff, nutrients, and sediments to inshore waters (Guilcher, 1988)
2. The pattern of relative sea-level change (the combined influence of sea-level change and tectonic stability) during the postglacial transgression (see *Postglacial Transgression*) (Adey, 1978), which together with the topography of the substrate provides the accommodation space (see *Accommodation Space*) in which a fringing reef may grow (e.g., Tudhope and Scoffin, 1994; Smithers et al., 2006)

The rate and mode of accretion at some fringing reefs has also been significantly affected by the regional storm



**Fringing Reefs, Figure 1** (a) Classic fringing reef growth *sensu* Darwin; (b) incipient fringing reef growth and development (After Chappell et al., 1983).

climate (e.g., Blanchon et al., 1997; Braithwaite et al., 2000) (see *Tropical Cyclone/Hurricane*). These factors combine to produce fringing reefs that may on the surface appear simple (as described by Stoddart and Steers, 1977), but which morphostratigraphic and geochronological investigations of a broad sample of fringing reefs from around the world show may be produced by a variety of different growth models. The aims of this short review are to examine the main factors that control fringing reef development in its various modes and to describe the main features common to most fringing reefs.

### Fringing reefs and terrestrial influence

By definition fringing reefs are closely associated with adjacent landmasses. These landmasses fundamentally influence fringing reef development by providing the substrate on which most develop. Another consequence of this relationship is, however, that fringing reefs are more directly exposed to freshwater, nutrients, and sediments – natural and anthropogenic – shed from coastal catchments, which may inhibit coral growth (e.g., Cortes et al., 1994; Furnas, 2003; McCulloch et al., 2003; Fabricius, 2005) and influence reef development (e.g., Bellwood et al., 2004). The nature of these interactions is outlined below.

### Fringing reef substrates

Many fringing reefs do grow over rocky substrates as suggested in classic models of fringing reef development. In mid-ocean settings, drilling (see *Drilling*) through the entire reef sequence has, for example, established volcanic foundations for the fringing reef at Hanauma Bay, Oahu, Hawaii (Easton and Olson, 1976) and at Pointe-au-Sable Reef, Mauritius (Montaggioni and Faure, 1997). On high islands and mainland coasts bedrock foundations for fringing reefs have similarly been established (e.g., at the north and northeastern end of Grand Terre, New Caledonia [Cabioch et al., 1999], at Phuket [Scoffin and Le Tissier, 1998], and at Punta Islotes, Costa Rica [Cortes et al., 1994]). The suitability of these stable substrates for coral colonization and reef growth is demonstrated by the rapidity with which reefs form on recent volcanic islands; Umbgrove (1930) described incipient fringing reef growth at Krakatoa less than 50 years after its catastrophic eruption (see *Volcanic Disturbances and Coral Reefs*). Although rock substrates are widely perceived as optimal for reef initiation and growth due to their stability and elevation above the sea floor (Veron, 1995), on the GBR where more than 25 fringing reefs have been cored – only at Scawfell Island on the southern GBR is the possibility of a bedrock foundation suggested, despite the widespread availability of headlands (Kleypas, 1991).

As additional coring data from fringing reefs have become available it is evermore apparent that fringing reefs can rise from a variety of foundations. Although fringing reefs less commonly develop over Last Interglacial (LIG) or older reefs (see *Last Interglacial and Reef Development*) than barrier reefs or atolls, drilling

has confirmed a pre-Holocene reefal basement for many fringing reefs including Australia's largest fringing reef – Ningaloo Reef, Western Australia (Collins et al., 2004), fringing reefs in the Ryukyu Islands of Japan (Kan et al., 1995; Webster et al., 1998), those on the south and southwestern shores of Grande Terre, New Caledonia (Cabioch et al., 1999), and for many fringing reefs throughout the Caribbean (e.g., Milliman, 1973; Hubbard et al., 2005). Different carbonate deposits of varying age underlie other fringing reefs, including Miocene calcareous siltstones at Galeta Point, Panama (Macintyre and Glynn, 1976), and eolianites at Lord Howe Island (Woodroffe et al., 2005) (see *Eolianite*).

The occurrence of unconsolidated sediments, often very fine, on the seafloor in nearshore environments is not unexpected given the proximity to fluvial and other sources. However, the frequency with which fringing reefs have grown over these foundations is more surprising given the difficulties that such substrates present for coral settlement and growth (see *Corals: Environmental Controls on Growth*). Nonetheless cores through many Holocene fringing reef sequences terminate in either Holocene siliciclastic deposits, sometimes mixed with reefal carbonates (Perry, 2003; Perry and Smithers, 2006), or in Pleistocene clays (Hopley et al., 1983; Perry and Smithers, 2010). In several instances fringing reefs have established on deltaic deposits of alluvial cobbles (Partain and Hopley, 1989) where fluvial discharge of water and sediments have clearly in the past been significant (see *Turbid Zone and Terrigenous Sediment-Influenced Reefs*), and at others Pleistocene boulder beaches appear to have been colonized by reefs in the Holocene (Hopley and Barnes, 1985; Perry and Smithers, 2009) (see *Boulder Beaches*).

The topography and spatial extent of the substrate can exert considerable influence on fringing reef morphology and geometry (Davies and Marshall, 1979), although the effects of both usually diminish with time (Macintyre and Glynn, 1976). At the most basic, on steep shorelines the extent to which the fringing reef may prograde seaward is limited by the depth of the foundations so that typically narrow reefs develop – vigorous reef growth is restricted to within 50 m or so of the surface (see *Corals: Environmental Controls on Growth*). In contrast, where the substrate is more gently sloping, the reef may construct a broad reef flat extending hundreds of meters offshore. As discussed in section “Fringing reef structure and growth models,” particularly on shallow gradient substrates fringing reefs may grow in complex ways and diverge significantly from the Darwin's classic simple model of seaward progradation from the shore. On more gently sloping coasts fringing reefs may initiate over a relatively broad area if suitable substrate is available, so that a diffuse “incipient reef” comprised initially of separate patch reefs may coalesce to form a more substantial fringing reef structure (Figure 1b). Chappell et al. (1983) suggested these models could accommodate many fringing reefs of the GBR, but they clearly have wider



application (as do a variety of other fringing reef growth models outlined in section “Fringing reef structure and growth models”).

The majority of fringing reefs can be broadly classified as one of the four main types on the basis of their coastal setting:

1. Headland/rocky shore-attached fringing reefs (Figure 2a).
2. Bayhead fringing reefs that develop in embayments and prograde out from the head of the bay (Figure 2b).
3. Beach base fringing reefs that develop along linear stretches of often sandy coasts (Figure 2c).
4. Nearshore shoals which can occur in all of the above coastal settings, but are not directly attached to the shoreline (Figure 2d). The water depth separating these reefs from the shore will be less than 10 m, satisfying the definition of a fringing reef, but they may become “true” fringing reefs if the coast progrades onto the leeward reef margin, as inferred at Yule Point, on the northern GBR (Bird, 1971).

This simple classification scheme requires little explanation. However, any particular fringing reef, or section of it, may display characteristics transitional between more than one class, both in space and through time. For example, at Paluma Shoals on the central GBR the northern shoal is attached to the shoreline by intertidal sand flats

and is a “beach base” fringing reef, but the southern shoal is presently separated from the shoreline and is a nearshore shoal (Figure 2d). It is also important to recognize that the terrestrial (and marine) influences affecting fringing reefs in each of these settings may differ, and will affect reef development. Drilling results show that many fringing reefs have accumulated over foundations of several different types (e.g., Hopley et al., 1978, 1983; Camoin et al., 1997), and establish that a basal reef rubble unit is common above the pre-reefal substrate. This suggests that once some fringing reefs have established fore reef talus (e.g., Tudhope and Scoffin, 1994) and/or detrital clasts washed to leeward (e.g., Easton and Olson, 1976; see Hopley et al., 2007) may accumulate and provide a substrate on which later reef growth may proceed. However, this process cannot proceed indefinitely, with fringing reefs prograding more slowly when the rate at which detrital basal deposits are formed or preserved is diminished. For example, the ages of fossil microatolls (see *Microatoll*) across the reef flats of bayhead fringing reefs on the GBR show that many rapidly prograded to fill most of the enclosing bays between around 6,500 and 2,000 years ago, but have accreted very little in the past few millennia (Smithers et al., 2006). This probably reflects two factors – the shutdown of vertical reef growth and sediment supply as a result of relative sea-level fall during the late Holocene, and reduced retention of



**Fringing Reefs, Figure 2** (a) Headland/rocky shore-attached fringing reef, Murray Island, Torres Strait; (b) bayhead fringing reef, Pioneer Bay, Orpheus Island, GBR; (c) narrow beach base fringing reef, Cape Tribulation, GBR; (d) nearshore shoal, Paluma Shoals, GBR.

sediments at the reef edge due to greater exposure to longshore currents at the mouth of the embayment, where ongoing seaward progradation is now constrained by the same processes that have limited substantial fringing reef development on the adjacent headlands.

A review of the available chronostratigraphic data available for fringing reefs indicates that most began to form soon after the sea inundated the substrate during the postglacial transgression, and that the bulk of most fringing reef frameworks were in place within a few thousand years (Kennedy and Woodroffe, 2002; Montaggioni, 2005; Hopley et al., 2007). Where later start-ups have occurred it is likely that the substrate is only recently available, due perhaps to shoreline movement or migration of shallow marine sediment deposits (Larcombe and Woolfe, 1999; Perry, 2005), and/or the environment is very marginal and reef growth is episodic. Although the details of why some apparently suitable substrates are not colonized by fringing reefs while some very marginal substrates are remain unknown, the rapidity with which corals have colonized most suitable coastal substrates and have developed fringing reefs has been observed at sites of recent volcanic activity (Umbgrove, 1930) and is demonstrated by the weight of radiometric dates from basal units in fringing reef cores (see *Radiocarbon ( $^{14}\text{C}$ ): Dating and Corals*). On this basis it would seem logical to suggest that substantial fringing reefs have probably already established at most sites that they are likely to.

#### Influence of terrestrial runoff, sediments and nutrients on fringing reefs

The environmental conditions required for coral growth are necessary prerequisites for fringing reef development, and where these conditions are not met or are marginal, fringing reefs will be absent or poorly developed. At a broad scale this is most markedly expressed on tropical coasts near major rivers where massive freshwater plumes and sediment flux have limited fringing reef development, such as in the western Atlantic south of around 5°N where the influence of the Amazon is felt, or adjacent to the Mekong, Niger, Congo, and Irrawaddy Rivers where fringing reefs are similarly lacking (Hopley, 1982). In addition to controlling fringing reef distribution, where reefs can grow, terrestrial runoff and associated sediments and nutrients may also affect fringing reef development and morphology.

Guilcher (1988) distinguished a range of fringing reef “subtypes” according to the extent of development of a deeper back-reef channel termed the “boat channel” (see *Boat Channel*) – a depression less than 10 m deep between the shore and the outer reef flat that is commonly used for small boat traffic on reef coasts. It was Guilcher’s view that the boat channel formed because coral growth was suppressed relative to that closer to the outer reef edge, most probably by freshwater, nutrients, and sediments shed from the adjacent landmass. Water may also be ponded over the backreef in moats (see *Moats*), but

moats form where the ebbing tide is held over the reef flat (see *Reef Flats*) rather than in depressions produced where upward reef growth is inhibited. Guilcher (1988) proposed that the simplest fringing reefs were shore-attached and lacked a boat channel, and developed where terrestrial impacts on reef growth were minimal, as occurs in semi-arid areas such as in the Red Sea. As discussed in section “Fringing reef growth and sea level,” this view is oversimplistic as it does not consider the influence of relative sea-level history. Fringing reefs with incipient boat channels comprise another subtype, with a shallow (<2 m deep) navigable channel behind the reef crest, with scattered live corals but generally only limited sediment accumulation indicative of minor terrestrial runoff. These reefs are common in the Gulf of Aqaba, but reefs from the Seychelles, Sri Lanka and Madagascar may also be included in this subtype (Guilcher, 1988). Fringing reefs with well-developed boat channels – several meters deeper than the reef flat and up to several hundred meters wide – can also be recognized, for example, at Lord Howe Island in the Tasman Sea (Figure 3), and along the southwest coast of Madagascar. Finally, the most complex subtype described by Guilcher (1988) is fringing reefs with multiple land-locked lagoons – which he attributes to the combination of a wide intertidal zone and macrotidal range.

The influence of the adjacent landmass on fringing reef growth is well demonstrated on the GBR where fringing reefs are the most common reef type (758 of 2,904 named reefs [26.1%]) but significant development on the mainland coast is restricted to the rocky shores of the Whitsunday region, and then intermittently north of Cairns (Hopley et al., 2007). Elsewhere, coastal sediment dynamics, high seasonal fluvial yields from large coastal catchments, and high inshore turbidity associated with wind-wave resuspension of the inshore sediment prism (Woolfe and Larcombe, 1999) inhibit fringing reef initiation and growth (Hopley et al., 2007). Fine sediments may be resuspended very quickly by waves – at Nelly Bay, Magnetic Island, wave-driven turbidity increases of three orders of magnitude up to 100 NTU (Nephelometer Turbidity Units) have been measured in an hour (Orpin et al., 2004) (see *Turbid Zone and Terrigenous Sediment-Influenced Reefs*). Most fringing reefs on the GBR (652 of 758 [86%]) occur on high islands offshore from the mainland, although fringing reef development can be poor on those closer inshore. Fringing reef development is also poor on larger high islands such as Hinchinbrook Island and Gloucester Island where runoff can be substantial, but some large high islands do support good fringing reefs and so other controls must also be involved (Hopley, 1982). Although fringing reefs are abundant on the GBR they are generally relatively small (mean <1 km<sup>2</sup>), and a significant number (213 of 758 [28.1%]) are defined as “incipient” – indicating that they lack extensive reef flat development (Figure 1b). Although substrate geometry and other factors can restrict fringing reef size, the generally limited dimensions and development may also reflect their vulnerability to episodic disturbances such as flood



**Fringing Reefs, Figure 3** Lord Howe Island, Tasman Sea.

plumes that can produce mass mortality events from which recovery can be very slow, thus stunting reef growth potential. Luxuriant reefs offshore of Mackay photographed in the late 1880s that were killed by a cyclone-generated flood plume in 1918 had recovered little by 1982 (Hopley, 1982).

Sediment and nutrient delivery to coastal waters where fringing reefs grow has been linked to the degradation of many fringing reefs (e.g., Punta Islotes, Costa Rica [Cortes et al., 1994]; Rodrigues [Naim et al., 2000]; Seychelles [Jennings et al., 2000]), with impacts arising due to smothering and burial, elevated turbidity with loss of photosynthetic capacity and energetic costs, and increased competitiveness of fleshy macroalgae and shifts from a coral to algal-dominated ecosystem (Umar et al., 1998; Fabricius, 2005). For some fringing reefs sediment related impacts may be natural; for example, periodic shifts in the position of river mouths may affect fringing reef growth and potential growth areas (Cortes et al., 1994), and at a larger scale, two catchments draining into the GBR exceed 130,000 km<sup>2</sup> in area, and the total catchment area draining into the GBR is nearly 425,000 km<sup>2</sup>, and thus for significant stretches of the coast large inputs of sediment and runoff are experienced periodically during natural floods (Neil et al., 2002).

However, there are clearly thresholds of sediment and nutrient exposure above which corals are unlikely to survive to establish fringing reefs of significant size. Nevertheless, it is crucial to recognize that corals can adapt to these pressures and that critical thresholds vary with location. On the GBR, high terrestrial runoff, into a relatively low-energy and protected lagoon, routinely exposes corals on inshore fringing reefs to ambient levels of turbidity and sedimentation known to stress and possibly kill those on other reefs (Pastorok and Bilyard, 1985; Hopley et al., 2007), and stratigraphic evidence confirms that many fringing reefs have always grown under naturally turbid

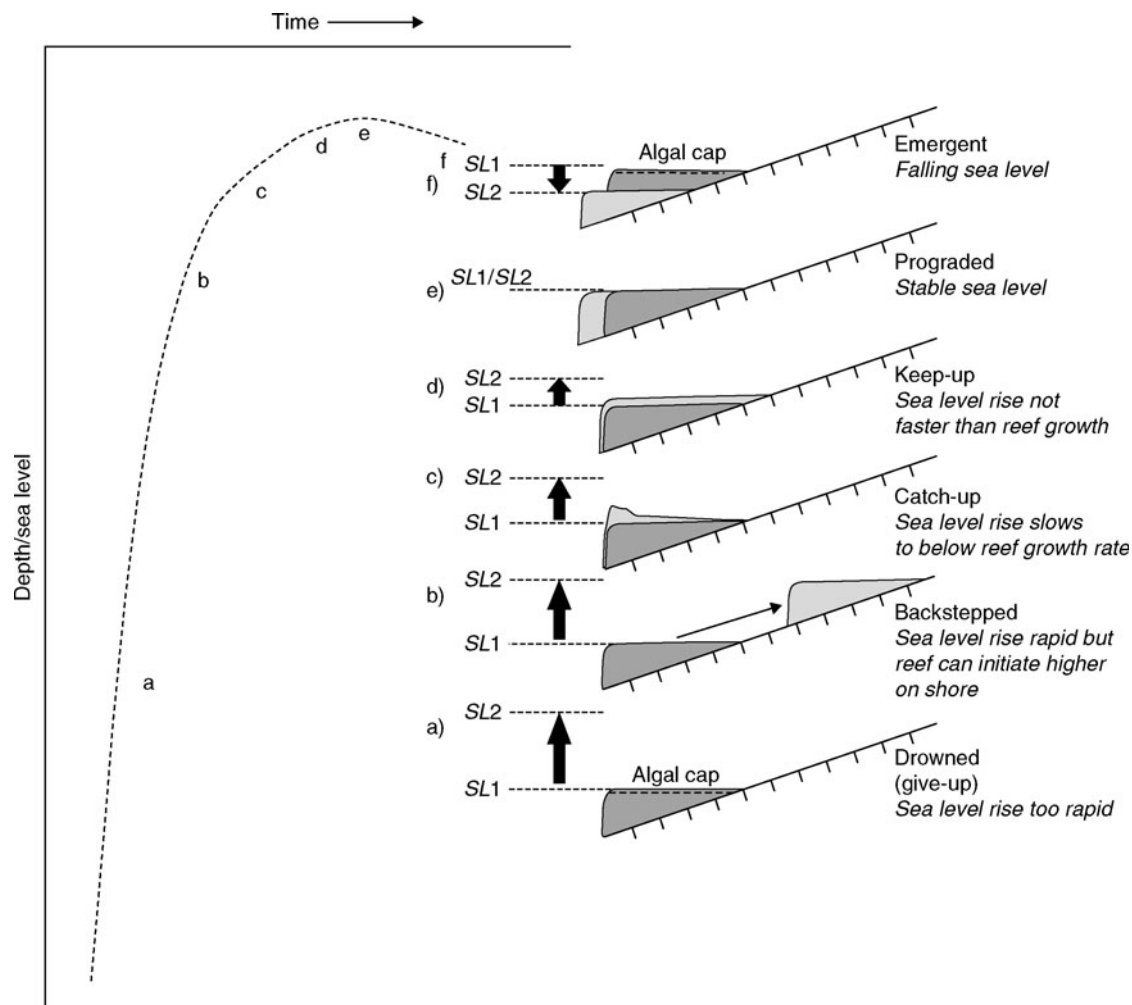
conditions (Smithers and Larcombe, 2003; Perry et al., 2008). Many corals on these reefs grow vigorously, and have adapted to these turbid conditions (Anthony, 2000, 2006). Paradoxically, however, the apparent vigor of reef corals does not appear to directly translate to continued reef accretion – most fringing and nearshore reefs have not added much to their structures for several thousand years (Smithers et al., 2006).

### Fringing reef growth and sea level

Holocene sea-level changes have been an important control on the development of all modern reefs (see *Sea Level Change and Its Effect on Reef Growth*), flooding substrates suitable for reef initiation and then providing the accommodation space into which fringing reefs may grow (see *Accommodation Space; Postglacial Transgression*). The timing of initiation is broadly governed by substrate depth, with deeper substrates flooded earliest and shallow substrates more recently. The amount of accommodation space available above any substrate depends on the rate of sea-level rise, the lag between inundation and initiation, and the rate of vertical reef accretion. These all vary from place to place. The timing of initiation and rates of vertical reef accretion are discussed in the following section on reef structure and growth models.

Geographic differences in the nature of Holocene sea-level changes related both to ocean volume and regional and local isostatic adjustments to the redistribution of mass (see *Glacio-Hydro Isostasy*) have produced different growth responses in fringing reefs, most of which reflect the balance between rates of vertical reef accretion and relative sea-level rise, the net result of which is available accommodation space. The range of reef responses is summarized in Figure 4 (modified from Woodroffe, 2002). Figure 4 presents sea-level change – reef growth scenarios that can explain some of the morphological





**Fringing Reefs, Figure 4** Fringing reef growth responses as a function of sea-level change (based on 5.11 Woodroffe).

differences between fringing reefs of the Indo-Pacific – where present sea level was generally reached around 6,000 years ago has since slowly fallen to present (see *Mid Holocene*) (Pirazzoli, 1991) – and the Caribbean, where sea level has risen to present at a decelerating rate, to reach its current position only recently (Lighty et al., 1982) (see *Western Atlantic/Caribbean, Coral Reefs*).

Reef flat morphology is the most conspicuous consequence of the varying sea-level histories experienced by fringing reefs in different locations. Throughout the Indo-Pacific fringing reefs with back-reef reef flats (see *Reef Flat*) that are dry at low tide are widespread, often but not always reflecting the late Holocene sea-level regression experienced in this region (see *Postglacial Transgression; Sea Level Change and Its Effect on Reef Growth*). In these locations the now emergent back reef formed when sea levels were higher in the mid-Holocene and the modern reef is confined at a lower level at the reef front (e.g., Chappell et al., 1983). In the Caribbean, where modern sea level has only recently been achieved (Lighty

et al., 1982), fringing reefs with shallowly submerged back reefs are more common. Adey (1978) speculated that the divergent back-reef morphologies were principally a function of sea-level history; he suggested that shallow lagoons developed on the Caribbean reefs where the more vigorously growing reef crest reached sea level before the back reef, confining a shallow lagoon over the back reef at low tides.

### Fringing reef structure and growth models

The growth histories of modern fringing reefs are documented by the materials and depositional fabrics preserved in their internal structures. Detailed stratigraphic and sedimentological investigations augmented by radiometric dating have enabled the growth histories of many fringing reefs to be interpreted, revealing details on age structure, past reef morphology, and the dominant processes of reef construction. Kennedy and Woodroffe (2002) reviewed the published literature on fringing reefs and

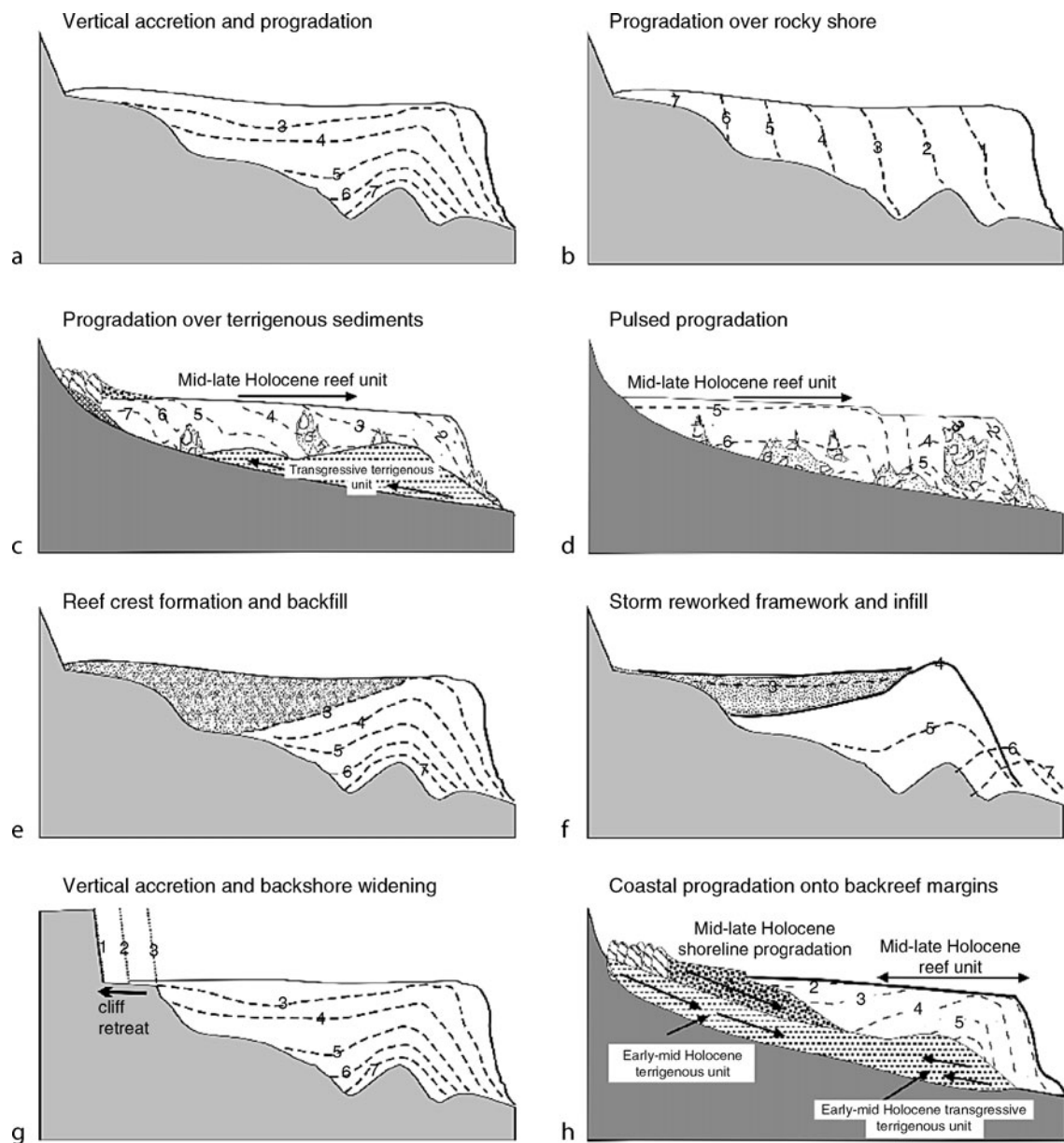
identified six generalized models of fringing reef development which are presented in Figure 5 and described below:

### Vertical accretion and progradation

Fringing reefs of this type typically initiated over a deeper substrate flooded earlier in the postglacial transgression at a point now nearer to the reef crest than the shore. Although vertical and lateral reef accretion is relatively slow and concentrated around the point of initiation for about 1,000 years, reef growth soon after spreads across

a broader area – mainly to leeward – and rapidly grows toward the surface, exhausting available accommodation space over most of the reef flat. The reef front vertically accretes at a more rapid rate than the backreef – probably due to poorer water quality, and seaward lateral progradation slows as the reef front moves into deeper water (Figure 5a).

This model of growth fits the pattern of fringing reef development established by two of the earliest but most detailed chronostratigraphic studies yet undertaken on



**Fringing Reefs, Figure 5** Fringing reef growth models: (a) vertical accretion and progradation; (b) progradation out from shore over rocky substrate; (c) progradation over terrigenous sediments; (d) pulsed progradation; (e) reef crest formation and backfill; (f) storm-reworked framework and infill; (g) vertical accretion and backshore widening; (h) coastal progradation onto backreef margin (Modified from Kennedy and Woodroffe, 2002; Smithers et al., 2006).

fringing reef structure – Easton and Olson's (1976) study of Hanauma Bay, Oahu, Hawaii (reef flat 90 m wide, 10 cores, 63 radiocarbon dates), and Macintyre and Glynn's (1976) study at Galeta Point, Panama (reef flat 200 m wide, 13 cores, 32 radiocarbon dates). At both reefs initiation occurred around 7,000 years ago – at Hanauma Bay over volcanic tuffs and basaltic sands, at Galeta Point over Miocene calcareous siltstones – and was dominated by massive corals. At both reefs, between 6,000 and 3,000 years ago, vertical accretion by rapidly growing coral frameworks took place, at Galeta Point dominated by *Acropora palmata*, which quickly masked any influence of the underlying topography (vertical accretion rates of between 1.3 and 10.8 mm year<sup>-1</sup> occurred during this phase). At Hanauma Bay, vertical accretion rates during this main phase of reef growth were slower, averaging around 2.9 mm year<sup>-1</sup>. After about 3,500 years BP at Hanauma Bay and 2,000 years BP at Galeta Point negligible vertical accretion occurred – with the reef at the former dominated by the coralline algae *Porolithon* and only scattered coral colonies, and the reef flat at Galeta Point now dominated by sea grass and *Halimeda* meadows. Grigg (1998) reports that the Hanauma Bay reef continues to prograde seaward at around 22 mm year<sup>-1</sup>. In contrast, despite its impressive growth between 6,000 and 3,000 years ago, Galeta Point fringing reef is now effectively senescent.

The similarity of reef growth evident at Hanauma Bay and Galeta Point is perhaps surprising given that they experienced different sea-level histories (see section “Fringing reef growth and sea level”). The dominance of *A. palmata* in the framework during the main phase of reef growth was interpreted by Macintyre and Glynn (1976) as evidence that Galeta Point was a keep-up reef able to keep pace with a sea level that rose at a decelerating rate to its present position. Easton and Olson (1976) also concluded that Hanauma Bay was a keep-up reef, but this interpretation has been challenged because they did not recognize evidence of higher sea level during the mid-Holocene (Grossman et al., 1998), and it is now generally agreed to be a catch-up rather than keep-up reef (Grigg, 1998).

On the GBR, Hayman Island is the only fringing reef for which data are available that loosely follows this model (Hopley et al., 1978). At Hayman Island the fringing reef developed over a gently sloping substrate of last interglacial limestone, now more than 1 km from the contemporary shoreline at a depth between –15 and –20 m, very soon after it was flooded by the transgression (the earliest dated coral above the substrate is 9,320 years BP). The interpretation is that original reef was outflanked by shoreline retreat and shoreline backstepping during the transgression, stranding it offshore as a catch-up reef. Once sea level stabilized in the mid-Holocene the reef caught up, and back-reef infilling and seaward progradation from the new shoreline combined to construct the reef flat. In this regard Hayman Island reef flat may also have some affinity to the reef crest and backfill model depicted in Figure 5e described further below (section “Reef crest and backfill”).

### Progradation out from shore over rocky substrate

Fringing reefs complying with this growth model initiate at the shoreline where they grow up to sea level and then prograde seaward (Figure 5b). This model of fringing reef development is most like the simple model conceived by Darwin (Figure 1a). However, detailed studies demonstrating that any particular reef has grown this way – over a hard bedrock shoreline are rare – Rees et al. (2006) inferred that the windward fringing reef at Lizard Island on the northern GBR grew directly over a granitic bedrock foundation and has prograded seaward, but from the three cores presented it is difficult to confidently determine the broader growth pattern. In Torres Strait, drilling reveals that reef initiation occurred close to shore at both Hammond and Yam Islands (Woodroffe et al., 2000), the former over a Pleistocene reef limestone at around 7,000 years ago and around 1,000 years later at Hammond Island, over a granite substrate but with significant mud deposition occurring during reef growth.

The northern section of the fringing reef at Iris Point, Orpheus Island, also on the GBR, rises over a rocky but unconsolidated foundation; drilling suggests the reef grows over a boulder beach (see *Boulder Beach*) comprised of corstones winnowed from the regolith. These boulders vary from 0.4 m to several meters *a*-axis length, and would be stable under normal conditions. At Iris Point reef initiation took place around 7,000 years ago and vertically accreted rapidly (4 mm year<sup>-1</sup>) to be constrained by sea level by 6,250 years ago, as indicated fossil microatoll ages (Hopley and Barnes, 1985) (see *Microatoll*). By 5,500 years BP the reef flat had begun to prograde seaward, and because sea levels were falling post highstand (Chappell et al., 1983), the reef flat was constrained at a lower level than the older reef flat to landward. Rates of seaward progradation at northern Iris Point have been estimated at between 50 and 500 mm year<sup>-1</sup>. Significantly, another transect at Iris Point located around 1,000 m to the south shows a different (younger) age structure and internal fabric, demonstrating the fact that a particular growth mode may be very localized, even within the same reef. The southern part of the Iris Point fringing reef has grown over detrital material shed from the northern section and distributed alongshore, and in contrast to the older section which is composed of 40–60% framework, the southern reef contains less than 20% *in situ* framework (Hopley and Barnes, 1985).

Although detailed chronostratigraphic studies of fringing reefs with this growth strategy are rare, there are many narrow fringing reefs attached to rocky headlands that appear to have formed in this way, at least at some stage of their evolution.

### Progradation over terrigenous sediments

This model of fringing reef growth is characterized by reefs developed over sedimentary structures including Pleistocene alluvial fans (e.g., Paluma Shoals, GBR [Smithers and Larcombe, 2003]), transgressionary sediment deposits



trapped in embayments (e.g., Pioneer Bay, Orpheus Island [Hopley et al., 1983]) leeward island spits (e.g., Rattlesnake Island, GBR [Hopley, 1982]), and deltaic gravels (e.g., Myall Reef, Cape Tribulation, GBR [Partain and Hopley, 1989]) (Figure 5c). Typically (but not exclusively) these reefs initiate near the shoreline in relatively shallow water and prograde seaward as vertical accommodation space is limited, often by late Holocene sea-level fall. In such cases, as the reef progrades into deeper water only the upper few meters of its internal structure may be distinctly reefal, with a shallow reef framework capping a detrital and often muddy deposit below. This is the case of many fringing reefs surrounding the high islands of the GBR and in Torres Strait (Woodroffe et al., 2000; Hopley et al., 2007), and this has also been documented for fringing reefs off Mozambique (Perry, 2005) and in South East Asia. Tudhope and Scoffin (1994) demonstrated that the fringing reef at Phuket, which is dominated by a *Porites* framework (see *Porites*), has prograded over mud by a process of block toppling at the reef front as sea level has fallen since the mid-Holocene.

### Pulsed progradation

This model includes fringing reefs developed by episodically building a new reef structure parallel to the existing reef front, and then backfilling the intervening space with unconsolidated reef sediments (Figure 5d). Antecedent topographic controls are inferred as a probable control of this accretion pattern, but other factors may also be involved. The fringing reef at Yam Island, Torres Strait has developed in this way, indicated by dated subsurface corals from cores and fossil microatolls across the reef flat (Woodroffe et al., 2000). A similar pattern of reef development is described at Mangaia in the Cook Islands where two separate reef crests occur over the reef flat – an older reef crest over the emergent inner reef flat and the younger lower reef crest to seaward; behind each lies a backreef filled with detrital sediment (Yonekura et al., 1988). Sea-level fall is proposed as the principal driving factor for this episodic accretion, with the first phase concluding around 4,000 years ago, and the younger reef crest forming 1.7 m below the first around 2,000 years later (Yonekura et al., 1988). At the resort reef on Dunk Island, GBR, two separate phases of reef development can also be identified, one between 7,000 and 4,500 years BP and another after 1,600 years. In this lower energy setting, reef growth in both phases occurred as massive colonies grew to sea level and inter-colony spaces were infilled with reef rubble and terrigenous sediment (Perry and Smithers, 2010).

### Reef crest and backfill

In this growth model the reef crest reaches sea level more rapidly than the backreef to form a shallow lagoon that is later infilled (Figure 5e). This mode of growth is inferred for fringing reefs in the West Indies where sea level has only recently been achieved (Adey, 1978; Kennedy and Woodroffe, 2002), but also appears relevant to fringing

reefs in areas where there is no evidence of higher Holocene sea levels or where reef growth rates have been slow so that fringing reefs have only recently been sea-level constrained. Coring from fringing reefs at Mauritius and the Seychelles in the Western Indian Ocean, for example, indicate growth histories of infill behind a reef crest that reached sea level first, forming a shallow backreef lagoon (Montaggioni and Faure, 1997; Braithwaite et al., 2000). Similarly, at Lord Howe Island, a high-latitude reef, the broad reef crest around 200 m wide reached sea level around 5,000 years ago forming backreef lagoon (around 2 km wide and averaging 1.5 m deep) that has been slowly infilling since (Kennedy and Woodroffe, 2000), and Kan et al. (1995) suggest the fringing reef at Minna Island, Japan has a comparable history, complying with this growth model.

### Storm-reworked framework and infill

This growth model occurs in storm affected settings, and involves the destruction and reworking of reef framework by episodic storms, between which detrital material may be stabilized and form the substrate for the next phase of reef construction by calcifying reef organisms (Figure 5f). This model has been argued to be applicable to the fringing reefs surrounding Grand Cayman (Blanchon and Jones, 1995; Blanchon et al., 1997); storms have been linked to fringing reef growth and morphology in the Seychelles (Braithwaite et al., 2000). An internal structure dominated by detrital carbonate clasts, often deposited in distinct units was interpreted as signifying the importance of episodic accretion events such as cyclones on normally low-energy inshore reefs on the GBR (Smithers and Larcombe, 2003; Perry and Smithers, 2006), and given the importance of detrital material in most fringing reef structures it is probable that this model will also fit other areas affected by episodic high-energy storms.

### Other models

The six models above are applicable to relatively stable and “typical” shorelines. Fringing reefs occur in other tectonic and physical settings where additional but less common modes of reef growth can occur. On tectonically rising or subsiding coastlines the effect is to reduce or increase the amount of accommodation space respectively. As discussed earlier, where accommodation space is limited – as may occur on uplifted coasts – progradation dominates, whereas subsidence at rates higher than vertical reef accretion provides increased accommodation space – and vertical accretion tends to dominate reef growth (see Figure 4). Cabioch et al.’s study (1999) of fringing reefs around Grand Terre, New Caledonia elegantly demonstrates these effects, with different parts of the coastline subsiding and uplifting at rapid and slow rates. Where subsidence is rapid, relatively thick Holocene reefs have developed, where subsidence is relatively slow, only thin Holocene reefs have developed, and where uplift has occurred Holocene reefs comprise only a thin

veneer over the seaward edge of a Pleistocene reefal substrate. Another mode of fringing reef development was described from China Reef, Japan, where a narrow fringing reef initiated on a narrow Pleistocene reef terrace at around  $-10$  m, approximately 7,000 years ago, kept up with sea-level rise to form a narrow reef flat that has increased in width not through seaward progradation, which is depth limited, but through scarp retreat of the backing cliff in this high energy location (Kan et al., 1995) (Figure 5g). In contrast, some fringing reefs may have begun as nearshore reefs that were not shore-attached, but coastal progradation has built the shoreline onto the leeward reef margins (Figure 5h) – this model was proposed for Yule Point Reef on the GBR, and may also apply to King Reef, located 200 km further south (Figure 6).

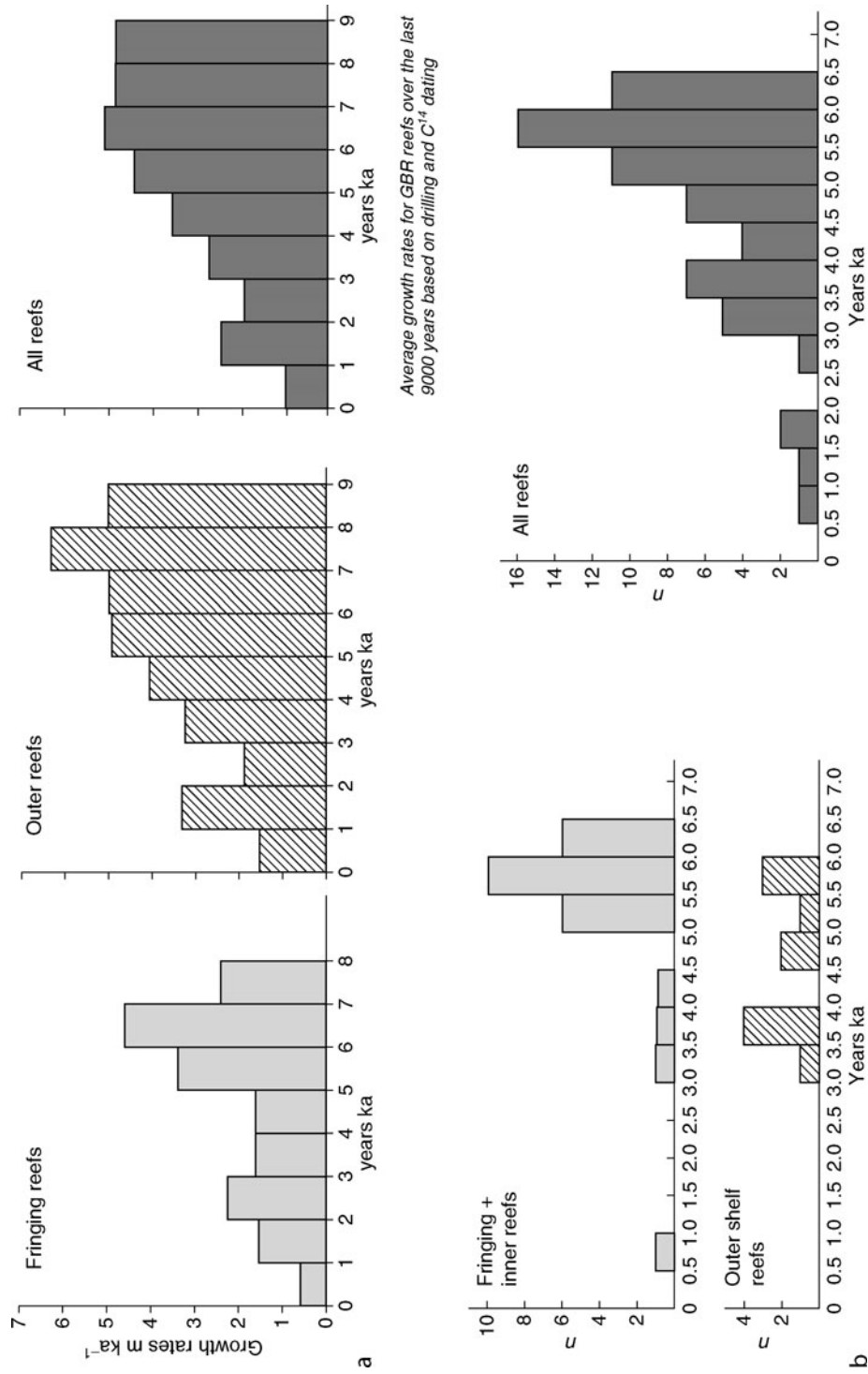
Although some variations exist due to differences in substrate depth, quality and the details of late Holocene sea-level history in particular, the general pattern of accretion history established for the GBR is broadly applicable to fringing reefs worldwide. Most fringing reefs on the GBR have accumulated a Holocene veneer of modest thickness, generally rising 5–10 m above their pre-Holocene foundations. Most reached sea level – or were within a few meters of it – between 7,000 and 5,000 years ago (Hopley et al., 2007) (and even in the Caribbean where modern sea level has only recently been reached, the bulk of many fringing reefs was emplaced over the same period). Vertical accretion rates of  $4\text{--}5\text{ mm year}^{-1}$  through this period are only marginally lower than the outer reefs (Figure 7). The most rapid growth is generally associated with catch-up phases on the GBR (and keep-up

phases in the Caribbean), with growth rates typically slowing in shallower water as accommodation space is reduced and hydrodynamic constraints associated with wave energy are experienced. Intrinsic and naturally reduced vertical accretion rates are common near the surface of reef cores from all over the GBR due to waves and other pressures (Davies and Hopley, 1983). However, higher rates are sustained to depths approaching 16 m at outer and mid-shelf reefs, but are restricted to a narrow depth window at  $\sim 4\text{--}8$  m below palaeosea-level on fringing reefs (Partain and Hopley, 1989). This possibly reflects the higher turbidity and sedimentation experienced at most fringing reefs compared to offshore reefs, and the reduced light-enhanced calcification at greater depths, especially in areas of higher tidal range.

Relatively little fringing reef development has occurred in the past few millennia, even where apparently healthy coral communities have occupied fringing reef slopes, and recent growth has mainly been limited to nearshore turbid-zone reefs initiating on newly exhumed substrates (Smithers et al., 2006). This age structure was established for many fringing reefs of the Central GBR by early research by Hopley (1982), and was confirmed as a broader regional trend by Chappell et al. (1983) who dated fossil microatolls across seaward sloping fringing reef flats through the Northern and Central GBR. Davies and Hopley (1983) noted that fringing reefs had a bimodal detrital accretion rate, with a lower range of  $1\text{--}5\text{ mm year}^{-1}$  associated with ambient conditions but a very rapid rate of up to  $15\text{ mm year}^{-1}$  attributed to rare high magnitude storm events. Rapid rates of vertical accretion associated with storms have been reported on fringing reefs in various



**Fringing Reefs, Figure 6** King Reef, Central GBR. Fringing reef initiated offshore with progradational coastline behind.



**Fringing Reefs, Figure 7** Fringing reef growth rates and sea-level constraint age on the GBR (Modified from Hopley et al., 2007).



locations around the world (e.g., Grand Cayman Island – Blanchon et al., 1997; Seychelles – Braithwaite et al., 2000). The importance of storm detritus versus *in situ* reef framework in fringing reef construction, and natural variability in both vertical and lateral rates of fringing reef growth are raising challenging questions about measuring and monitoring reef growth, destruction and condition to establish baselines in the face of projected environmental changes (e.g., Smithers et al., 2006).

### Fringing reef morphology and processes

Where fringing reefs have formed reef flats, their surface morphology is usually simple, comprising three main zones – a forereef, a reef crest, and a backreef. Fringing reef morphology can vary, however, over a single reef and from reef to reef, with the greatest complexity usually developed where the reef flat (see [Reef Flats](#)) includes sections formed during and after the mid-Holocene highstand (see section “Fringing reef growth and sea level”). Hopley and Barnes (1985) described seven geomorphological zones (see [Geomorphic Zonation](#)) on the northern section of the reef flat at Iris Point, Orpheus Island, GBR, the higher inner part of which reached sea level in the mid-Holocene (based on a 6,250 year old reef flat *Favid*). Only five zones were discriminated on the younger (near surface date: 3,780 years BP) southern section of the reef flat ([Figure 8](#)). Although the descriptions below are derived from a higher energy fringing reef on the GBR, the morphological zones discussed below may to varying degrees and combinations be found on many fringing reefs worldwide.

#### High water shingle and debris

An irregular ridge of mainly *Acropora* shingle to 10 cm length but also including other reefal debris, pumice and flotsam is deposited at the highest level of contemporary storm activity (see [Shingle Ridges](#)). This ridge can rise to over a meter in height, and usually has a steep seaward face. The lee side is often less abrupt, and can include small fans or splays. In more protected locations this zone may be replaced by a sandy beach, as occurs at nearby Pioneer Bay (Hopley et al., 1983).

#### Terrigenous boulder beach

Rhyolite and basalt boulders form a beach around 35 m wide that lies behind the reef flat. The lower boulder beach is cemented but the upper beach, which extends to the highest tidemark, is not. *In situ* corals indicative of a higher (~1 m) sea level in the mid-Holocene are attached to the boulder beach (Hopley and Barnes, 1985) in a manner comparable to that recently described at Dunk Island (Perry and Smithers, 2009). In other settings, a sandy beach, possibly with beach rock exposed, may replace the boulder beach (see [Beach Rock](#)).

#### Inner moat

A moated pool extends from the base of the boulder beach seaward to the shingle rampart (see [Moats; Moating](#)). At low tide water 0.3 m deep remains within the moated pool, >1 m above the open water low tide level. Corals including *Porites* and *Goniastrea* microatolls survive in this moat. A veneer of poorly sorted carbonate sediments floors much of the moat, with abundant rhodoliths (see [Rhodoliths](#)) accumulating at the landward edge. This zone is typical of fringing reef flats partly formed during higher mid-Holocene sea level, but can also occur where uplift has occurred or high-energy storms are common.

#### Shingle rampart

A shingle rampart to 0.3 m high and around 10 m wide was located at the seaward edge of the inner moat when Hopley and Barnes (1985) mapped the reef flat, but much of it has since been destroyed. This feature is formed when rubble is thrown onto the reef flat by storms, and similar features are common on other fringing reefs exposed to these events. Subtle bassett edges are sporadically preserved that document the former extent and position of the rampart at Iris Point (see [Bassett Edges; Shingle Ridges](#)).

#### Algal terraces

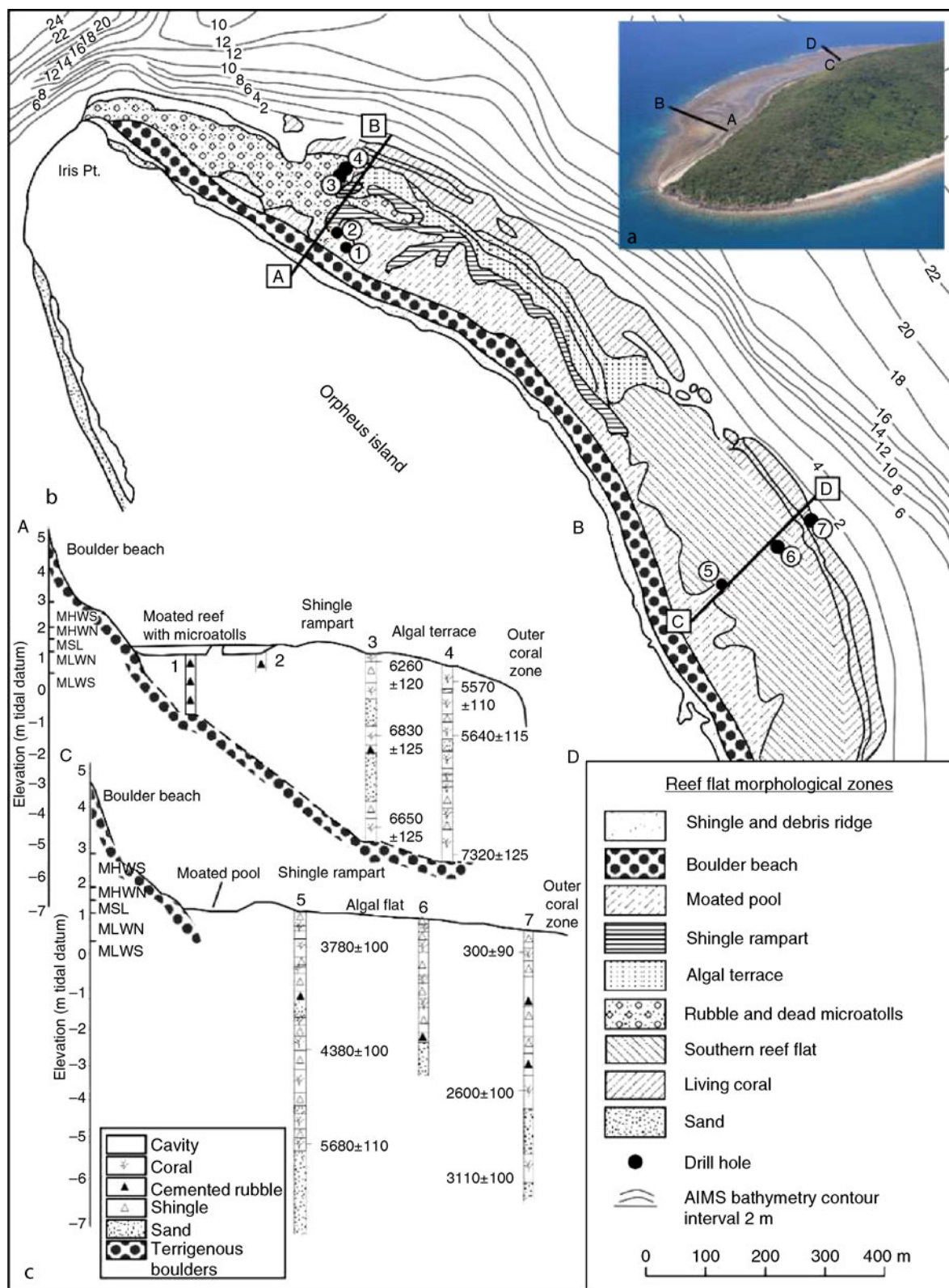
An algal pavement forms a relatively smooth feature that slopes down from the higher inner reef flat and shingle rampart to the lower outer living coral zone along most of the northern part of the reef flat at Iris Point. Crustose coralline algae (see [Algae, Coralline](#)) forms patches of this pavement, but it is mostly composed of *Acropora* shingle that has been stabilized with a filamentous turf algae (see [Algae, Turf](#)). Within this algal turf matting foraminiferans such as *Amphistegina*, *Calcarina*, and *Baculogypsina* are produced in great abundance (see [Foraminifera](#)). This feature is comparable with the algal-cemented pavements that are common on fringing reef flat across the Indo-Pacific.

#### Northern fossil microatolls

A pavement of coalesced fossil microatolls, some reaching 3 m in diameter, is located on the outer northern part of the reef flat at Iris Point. The tops of these microatolls are elevated ~0.8 m above their modern open water counterparts. There is no evidence that these microatolls have been moated, and they are therefore presumed to have formed at a higher sea level.

#### Amorphous southern reef flat

This zone is developed where the reef achieves its greatest width, and essentially consists of a relatively uniform, gently sloping surface of coral rubble bound by pink crustose coralline algae on its outer half and filamentous brown algae on the inner half. Radiocarbon dates indicate that this section of the reef flat was constructed after the mid-Holocene highstand. Hopley and Barnes (1985)



**Fringing Reefs, Figure 8** Iris Point fringing reef: (a) oblique photograph; (b) surface morphology; and (c) internal structure and chronostratigraphy (After Hopley and Barnes, 1985).

speculated that this possibly accounted for the morphological simplicity of this section of the reef flat.

### Outer living coral zone and reef slope

Live coral cover and biodiversity increases below mean low water springs on the outer reef flat. Soft corals (*Lobophyton*, *Sinularia*) and massive or head corals such as *Porites* and *Goniastrea* dominate at the rear of this zone, with *Acropora* becoming more abundant toward the reef crest. Patch reefs seaward of the crest are sporadically distributed along the reef front.

The physical processes operating of fringing reefs are covered in other entries and are not repeated here (see *Fringing Reef Circulation; Hydrodynamics of Coral Reef Ecosystems; Reef Flats; Reef Front Wave Energy; Wave Set-Up; Waves and Wave-Driven Currents*). It is more important to reemphasize that fringing reefs are exposed to particular processes due to their proximity to land, such as flood plumes (Devlin et al., 2001) and turbidity and sediment influx (Cortes et al., 1994; Wolanski et al., 2005), which may complicate the marine processes that structure reefs further offshore. Debate about the impacts of terrestrial exports on reef health is ongoing. It is, however, relevant to emphasize that many fringing reefs are (1) growing at their environmental extremes, and (2) are relatively old features at the “mature to senile end of the evolutionary spectrum” (see *Reef Classification by Hopley (1982)*). Although the pressures facing fringing reefs may have increased during recent times due to anthropogenic activities, it is critical to note that many fringing reef flats have been largely dead for thousands of years due to late Holocene sea-level fall (see section “Fringing reef growth and sea level”), and the net calcium carbonate productivity of most fringing reef reef-slope communities has been insufficient to enable significant lateral accretion for several thousand years (e.g., Smithers et al., 2006). The vulnerability of fringing reef flat communities, natural perturbations must be recognized when assessing the significance and causes of changes in reef flat community status; for example, reef flat coral communities surviving in moats at Holbourne Island, GBR suffered significant mortality when the confining rampart was breached by a cyclone in 1918 (Hopley and Isdale, 1977), lowering water levels by 40 cm, and as discussed in section “Fringing reefs and terrestrial influence” of this entry, natural movements in stream mouth position can directly impact on fringing reefs as documented at Punta Islotes, Costa Rica (Cortes et al., 1994).

### Summary

Fringing reefs are shore-attached and are exposed to a variety of pressures and processes related to this association that can affect their development. Although most fringing reefs are morphologically simple, their morphologies may become more complex where they incorporate reef flats formed at higher mid-Holocene sea levels, and where terrestrial inputs and processes affect them. The

apparent geomorphological simplicity of many fringing reefs masks development histories and internal structures that can be complex and diverse – fringing reefs develop over a range of foundations and are constructed of a variety of materials deposited in numerous arrangements (Figure 5). Of course, reefs are three-dimensional structures, and structural variation may occur within a single fringing reef. Although geographical variation exists due to differences in Holocene sea-level history and substrate availability, most fringing reefs experienced a period of active growth from 7,000 to 5,000 years ago when they produced most of their structure. On many fringing reefs living coral is now restricted to a narrow band near the seaward reef edge.

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## Cross-references

Accommodation Space  
 Algae, Coralline  
 Algae, Turf  
 Barrier Reef (Ribbon Reef)  
 Bassett Edges  
 Beach Rock  
 Boulder Beaches  
 Corals: Environmental Controls on Growth  
 Darwin, Charles (1809–1882)  
 Eolianite  
 Foraminifera  
 Fringing Reef Circulation  
 Geomorphic Zonation  
 Glacio-Hydro Isostasy  
 Great Barrier Reef: Origin, Evolution, and Modern Development  
 Halimeda  
 Hydrodynamics of Coral Reef Systems  
 Last Interglacial and Reef Development  
 Microatoll  
 Moats  
 Moating  
 Nutrient Pollution/Eutrophication  
 Postglacial Transgression  
 Radiocarbon (<sup>14</sup>C): Dating and Corals  
 Reef Classification by Hopley (1982)  
 Reef Drilling  
 Reef Flats  
 Reef Front Wave Energy  
 Rhodoliths  
 Sea Level Change and Its Effect on Reef Growth  
 Shingle Ridges  
 Subsidence Hypothesis of Reef Development  
 Tropical Cyclone/Hurricane  
 Turbid-Zone and Terrigenous Sediment-Influenced Reefs  
 Volcanic Disturbances and Coral Reefs  
 Wave Set-Up  
 Waves and Wave-Driven Currents  
 Western Atlantic/Caribbean, Coral Reefs

## FUNAFUTI ATOLL

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## Synonyms

Ellice Island; The main island of Tuvalu

## Definition

An atoll of Tuvalu located in the tropical South Pacific.

## Introduction

Funafuti Atoll (8°31' S, 179°12' E) forms a part of the Tuvalu Group (formerly the Ellice Islands). It is a typical atoll composed of ~33 reef islands (a total land area of 2.4 km<sup>2</sup>) and a lagoon of ~18-km diameter (275 km<sup>2</sup>). The islands are formed from fossil coral limestone and calcareous marine carbonates, particularly larger foraminifera. The lagoon has three main deep channels. Additional lagoon/ocean water interchange takes place over the reef rim, especially on the western side where the islets are small and widely separated. A total of 36 species of coral were recorded in 1983 and the blue coral *Heliopora coerulea* was abundant on the western rim (Buckley, 1985). A variety of corals occur on the reef slope and reef buttresses including *Acropora*, *Pocillopora*, *Montipora*, *Millepora*, *Acanthastrea*, *Favia*, etc. Over 200 fish species and 400 mollusks have been identified from the lagoon (UNEP, 1988). In the shallow lagoon, larger foraminifera are the dominant component of sand and gravel, while *Halimeda* replaces the foraminifera in deeper water (Collen and Garton, 2004). There are abundant coral reef fauna in the lagoon and on the reef.

The capital of Tuvalu is located on Fongafale islet, the main island of the atoll. Four thousand four hundred and ninety two people live on Funafuti Atoll (2002 Census). The total national population of Tuvalu is 11,126 in 2007 (<http://www.spc.int/prism/country/tv/stats/>). While tropical cyclones (recorded in 1891, 1958, 1972, and 1997) have destroyed many buildings on Funafuti, they have also played a significant role in land formation by re-sedimentation of submarine carbonates (Maragos et al., 1973). Recently, floods on Funafuti, especially on Fongafale islet during spring high tides were possibly associated with sea-level rise caused by global warming (Patel, 2006). More than 100 years ago, the Royal Society of London mounted an expedition to Funafuti Atoll to test Darwin's theory of the formation of coral atolls (Royal Society, 1904). The IUCN Conservation Monitoring Centre book, *Coral Reefs of the World*, provides useful information of Funafuti (UNEP, 1988). Also, over 1,000 references concerning the geology and biology of Tuvalu are indexed and annotated by Rodgers and Cantrell (1988).

## The Royal Society Coral Reef Expeditions

In 1896–1898, under the leadership of Professor Tannant Edgeworth David (Sydney University), the Royal Society drilled a 339-m drill hole on Funafuti Atoll to carry out the experiment desired by Darwin to interpret the origin and history of coral reefs (Darwin, 1842; The Royal Society, 1904; Grimsdale, 1952). But, the drilling did not reach the base of the atoll; however, it showed clearly that shallow water limestone over such a thickness must have been accompanied by a subsidence. Subsequent, but much later drilling by the U.S.G.S. at Eniwetok and Bikini Atolls in the 1950s proved finally that at least some atolls also had volcanic basements (Emery et al., 1954; Ladd and Schlanger, 1960). Over a century after the Funafuti

Expedition, selected samples from the 339-m-long drill core (preserved at the Natural History Museum) have been dated using high-precision radiocarbon and Sr isotope measurements (Ohde et al., 2002). From the radiocarbon dating, the top 26.4 m of the core records the history of sea-level rise during the last 8,000 years. For the previous two million years, however, only the recent use of high-precision Sr isotopic data have made it possible to provide records of the Quaternary sea-level history preserved in the atoll carbonates. During the past 1.5 million years, more than 150 m of reef-lagoonal carbonate was deposited through an interaction between glacial/interglacial sea-level changes and plate subsidence. Sections of dolomite in the lower core (196–339 m) were formed through diagenetic alteration between one and two million years ago, possibly resulting from seawater percolation. The atoll sequence reflects the interaction between carbonate sedimentation, tectonic subsidence, and eustatic sea-level change, and potentially provides a two million-year record of environmental change.

## Holocene reef growth at Funafuti

Radiocarbon dating of fossil corals provides information on Holocene reef history at Funafuti. Three shallow borings were carried out on the reef-flat of Fongafale (Royal Society, 1904). The top 26.4 m of the main boring is mainly composed of corals, including the soft coral *Sinularia* sp. (Table 1). The predominant corals belong to the genera *Millepora*, *Heliopora*, *Pocillopora*, *Favia*, *Porites*, and *Montipora*. Nine coral aragonite coral samples from the core top were dated by the accelerator mass spectrometry (AMS) radiocarbon method and calibrated (Ohde et al., 2002). Table 1 shows that the Holocene-Pleistocene boundary is situated at a depth between 26.4 and 27.4 m. Using the cores preserved at the Natural

**Funafuti Atoll, Table 1** AMS radiocarbon ages of core top samples from the Main Boring at Funafuti Atoll (Royal Society, 1904) (Data are compiled from Ohde et al., 2002)

| Depth <sup>a</sup><br>(m) | Calcite<br>(%) | Age <sup>b</sup> (±1σ)<br>(cal year BP) | Coral species                    |
|---------------------------|----------------|-----------------------------------------|----------------------------------|
| 0.3                       | 0              | 2,550 (±180)                            | Cemented coral                   |
| 1.2                       | 0              | 2,520 (±190)                            | Coral fragments                  |
| 3.0                       | 0              | 3,460 (±140)                            | <i>Porites</i> sp.               |
| 4.6                       | 0              | 4,410 (±140)                            | <i>Heliopora coerulea</i>        |
| 11.9                      | 0              | 5,290 (±170)                            | <i>Favia fava</i>                |
| 15.2                      | 0              | 6,280 (±120)                            | <i>Porites</i> sp.               |
| 24.4                      | 0              | 7,580 (±170)                            | <i>Sinularia</i><br>(soft coral) |
| 26.4                      | <1             | 8,130 (±170)                            | <i>Heliopora coerulea</i>        |
| 27.4                      | 3              | 100,000 (±20,000) <sup>c</sup>          | Cemented coral                   |

<sup>a</sup>The top of the core is at 0-m altitude and depths correspond to distances below surface

<sup>b</sup>Radiocarbon dating calibrated by INTCAL98

<sup>c</sup>Determined by <sup>226</sup>Ra/<sup>238</sup>U method



History Museum, it was observed that a change of carbonate textures occurred at 26.4 m – from a fossil reef above to strongly cemented facies below. The reef has grown upward from 8,130 to ~2,500 years BP at a growth rate of 4.73 mm/year ( $26,400/[8,130-2,550]$ ), much higher than those recorded at Enewetak, Mururoa, and the Cook Islands, but similar to that of Barbados (Fairbanks et al., 1989). The reef growth of 26.4 m reflects the infill of accommodation space for new reef growth made by the glacial stage erosion of the last interglacial stage 5e, continuing subsidence and rising Holocene sea level.

### Reef Island formation: higher sea-level or storm impacts?

The Royal Society (1904) reported on the island morphology of Funafuti Atoll, declaring that the island ridges (~2 m altitude) were composed of unconsolidated coral rubble and associated carbonate sand and corals in growth position on top of reef flat. Such observations have been used to infer that parts of the islets were formed during a mid-Holocene highstand and a subsequent fall to modern sea level (Schofield, 1977; Dickinson, 1999). However, it is undeniable that Funafuti Atoll is low lying and vulnerable to tropical storms (Maragos et al., 1973). Unconsolidated materials on Funafuti islets may therefore represent amalgamated rubble sheets deposited by storm-wave washover of the islets and episodic formation of rubble ridges on the reef platform (Dickison, 1999). Radiocarbon dating of reef blocks (probable storm deposits) together with historical records have been used to compile a history of large tropical storms in Funafuti Atoll, indicating major storms occurred in 2,000, 1,600, 1,450, 1,050, and 600 conventional radiocarbon years ago (McLean, 1992, 2004). In October 1972, a huge rubble rampart 18-km long (~10% of the land area of the atoll) was suddenly formed at Funafuti during cyclone Bebe, the material derived from deeper water offshore. Tropical cyclones therefore play potentially important role in the land formation of atolls such as Funafuti (Maragos et al., 1973). Radiocarbon dating of cores and surface samples (Schofield, 1977) show that the land area was estimated to form ~2,000–1,000 years ago on the reef flat when the sea level reached modern level (Schofield, 1977; Yamano et al., 2007). Prehistoric human settlement of Funafuti was also assumed to be much more recent than other traditionally populated islands like Majuro Atoll, the Marshall Islands (Yamano et al., 2007). Low altitude atolls are in future at risk from coastal damage caused by tropical storms and sea-level rise associated with predicted global warming by anthropogenic activities (Woodroffe, 2008). Cyclone Bebe was called as the strongest cyclone these 100 years (Baines et al., 1974). However, the lowest barometric pressure of 954 mb recorded during the storm (Maragos et al., 1973) is not too low compared to typhoons occurring in the tropical western-north Pacific. Therefore, Funafuti is in future at risk of flooding and damage by projected stronger cyclones.

### Funafuti and predicted sea-level rise

Recently, widespread floods in the interior of Fongafale islet on Funafuti have frequently occurred during spring high tides. Patel (2006) reported that Funafuti people feel the floods are getting worse possibly associated with sea-level rise caused by global warming. The potentially huge impact of sea-level rise on the people of Funafuti should be evaluated from the best estimate of sea-level change and its associated uncertainty from the available data. Hunter (2002), using two sets of data, one from the University of Hawaii Sea Level Center and the other from the Australian National Tidal Facility, predicted a rise of 0.8 ( $\pm 1.9$ ) mm/year. Rejecting data affected by Southern Oscillation events, Hunter predicted a rise of 0.4 and 2 mm/year at a 68% probability level. This would represent a rise of 4–20 cm in 100 years and could significantly increase the frequency and depth of saltwater flooding and accelerate coastal erosion, threaten the local food and housing, and could make the country simply uninhabitable. Many Tuvaluans may become environmental refugees when the island is drowned by the sea-level rise (Mortreux and Barnett, 2009). Even greater difficulties will arise as a consequence of rising sea levels and increased intensity and/or frequency of high-energy cyclonic events. Both will impact an atoll ecosystems much changed by anthropogenic processes (e.g., construction of an airstrip over original mangroves).

In conclusion, low-lying islands such as Funafuti are, in future, at risk of coastal damage including erosion, inundation, coral bleaching, changes in fishery resources, and agricultural productivity (Woodroffe, 2008; Mortreux and Barnett, 2009). Such risks are likely derived from changes in the island ecosystems on which Funafuti people depend for their livelihoods and cultures. Short-term scientific observations show little evidence of sea-level rise in Funafuti (Patel, 2006), but the Government of Tuvalu has argued that there is a visual evidence of sea-level rise, through such consequences as increased erosion, flooding, and salinity (Connell, 2003) and that Funafuti Atoll is in future at risk from coastal damage caused by the sea-level rise associated with predicted global warming by anthropogenic activities.

### Summary

Funafuti Atoll was the site of the Royal Society Coral Reef Expeditions in 1896–1898. The 339-m core was drilled into the atoll (at 0-m altitude) on Fongafale islet to carry out the experiment outlined by Charles Darwin to elucidate the origin and history of atoll formation. From the radiocarbon dating, the top 26.4 m of the core records the history of sea-level rise during the last 8,000 years. Sr isotope stratigraphy of the core indicates that during the past 1.5 million years, more than 150 m of reef-lagoonal carbonate was deposited through interaction between sea-level change and plate subsidence. Dolomite in the lower core (196–340 m) was formed through diagenesis between one and two million years ago. Radiocarbon dates of the core-top

together with surface fossil corals suggest that the land areas in the atoll were formed on the reef flat about 2,000 to 1,000 years ago. In 1972, cyclone Bebe struck Funafuti and showed tropical storms also play a significant role in the land formation of the atoll. Recently, floods have often occurred on Fongafale islet during spring high tides. In future, Funafuti will suffer the ravages of both high-energy events and rising sea levels.

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## Cross-references

[Atoll Islands \(Motu\)](#)  
[Bikini Atoll, Marshall Islands](#)  
[Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity](#)  
[Climate Change: Increasing Storm Activity](#)  
[Darwin, Charles \(1809–1882\)](#)  
[David, Tannant Edgeworth \(1858–1934\)](#)  
[Dolomitization](#)  
[Enewetak Atoll, Marshall Islands](#)  
[Radiocarbon \(<sup>14</sup>C\): Dating and Corals](#)  
[Reef Drilling](#)  
[Royal Society of London](#)  
[Sea Level Change and Its Effect on Reef Growth](#)  
[Tropical Cyclone/Hurricane](#)

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## GARDINER, JOHN STANLEY (1872–1946)

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### Definition

An eminent British zoologist who is primarily recognized for his early work on reefs throughout the Indian Ocean but who was also a major influence on the 1928–1929 Great Barrier Reef Expedition from its inception through to review of its resultant publications.

Professor Stanley Gardiner was best known for his extensive expeditions into the Indian Ocean to study the flora and fauna of coral reefs and islands in the early 1900s. As a young man, he joined the Royal Society Expedition to Funafuti in the Ellice Islands in 1896 to assist the deep boring of an atoll and test the “subsidence theory” of reef origin proposed by Charles Darwin. On this trip, he also visited nearby Rotuma and Fiji carrying out preliminary experiments on coral nutrition and growth, the results of which made him one of the first scientists to question the role of coral symbiotic algae in these processes. During 1899–1900, 1905, and 1908, Gardiner undertook several expeditions into the Indian Ocean working in the Laccadives, Maldives, Chagos Archipelago, Farquhar, Providence, St. Pierre, and Mauritius. He was one of first scientists to provide detailed descriptions of the reefs of the Indian Ocean together with taxonomic details of their constituent corals as well as comments on their form and possible modes of origin.

Less well known is the fact that he was a key figure in the instigation of the 1928–1929 Great Barrier Reef Expedition; in the funding and appointment of C.M. Yonge as

its leader; in the development of the scientific programme; and in evaluation of scientific papers which resulted from the expedition’s activities.

Gardiner was elected to the Fellowship of the Royal Society of London in 1908 and in 1909 became Professor of Zoology at Cambridge. In 1929, he was awarded the Agassiz Medal of the National Academy of Sciences of the United States and while in the country he delivered a series of lectures on coral reefs at the Lowell Institute in Boston which were published a year later in a book entitled “Coral reefs and atolls.” In 1936, he was awarded the Linnean Medal of the Linnean Society and in 1945 the Darwin Medal of the Royal Society of London. Throughout his life, he promoted coral reef interests both within his Department and abroad. At home, he provided a laboratory for fellow reef scientists such as R.B. Seymour Sewell and Cyril Crossland while personally supervising George Matthai’s anatomical treatise on soft tissues of reef corals. He entertained overseas visitors in Cambridge and during his and his student’s visits to the United States engaged actively with Thomas Wayland Vaughan, Alfred Goldsborough Mayer, and Alexander Agassiz. His legacy to reef science was much more than descriptive studies from the Indian Ocean and included scientific and administrative steerage of the Great Barrier Reef Expedition which set the scene for a new phase in the development of reef science in the twentieth century.

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## Cross-references

[Indian Ocean Reefs](#)

## GENERAL EVOLUTION OF CARBONATE REEFS

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### Introduction

While modern coral reefs are sites of high biodiversity forming impressive wave-resistant structures in clear tropical waters, many other organisms are known to form diverse types of reefs in temperate, low-energy settings or in deep waters.

Reefs have developed on Earth for over 3.5 billion years, and a tremendous diversity of communities of skeletal and nonskeletal metazoans, plants, algae, and microbes as well as inorganic calcium carbonate precipitation processes have contributed to their formation during this time. Reefs have shown zonation in response to environmental gradients from their inception, and metazoan reefs have been differentiated into open surface and cryptic reef communities for their entire ~550 million-year history (Wood et al., 2002).

Ancient reefs were biologically constructed reliefs that grew on the seafloor that are now expressed as massive bodies of calcium carbonate rock surrounded by bedded strata (Figures 1 and 2). Some formed small isolated structures; others became sufficiently large so as to influence the regional oceanographic and sedimentological environment. However, as sites of in situ biological growth, they often

record abundant palaeoecological information lost from other types of communities, as well as data that can be used to unravel changing climate and oceanography over evolutionary timescales.

Given the diversity of ancient reefs and settings, a strict uniformitarian approach to understanding reef evolution has limited utility. Indeed, for decades there has been an ongoing debate as to what constitutes an ancient reef (see James, 1983; Fagerstrom, 1987; Geldsetzer et al., 1988; Wood, 1999; Stanley, 2001 for summaries). A general term often used for ancient reefs with no connotations as to processes of formation, size, or shape is carbonate buildup.

Many ancient reefs had fundamentally different ecological and environmental demands compared to modern coral reefs. But all reefs, regardless of the organisms that form them or where they grow, are controlled by factors that enable the biological occupation of space on the seafloor.

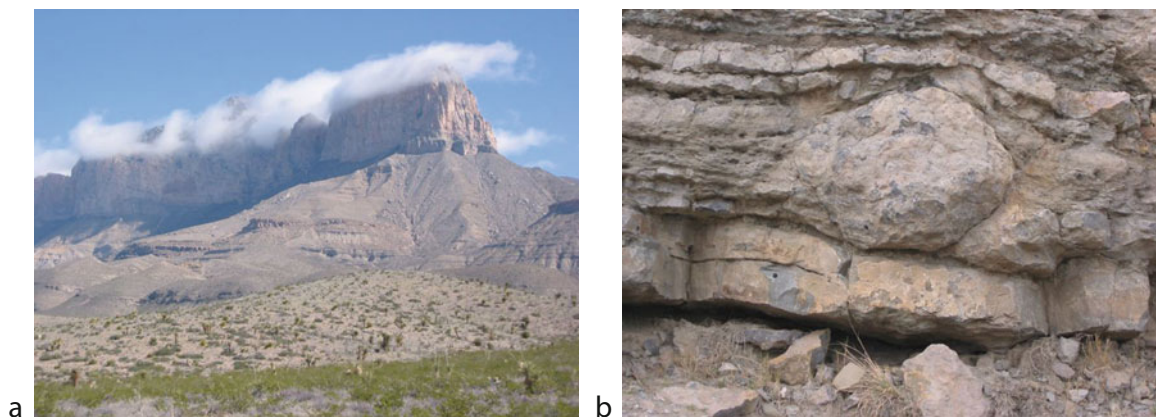
All reefs show the recurring processes of (1) in situ biological fixation of carbonate by organic assemblages of microbes, algae, and metazoans, (2) development of internal cavity systems during growth, (3) synsedimentary lithification, and (4) bioerosion (Figure 2). Reef evolution has recently been reviewed by James and Wood (2010), and the following review has been based in part upon this work.

### Biological fixation of carbonate

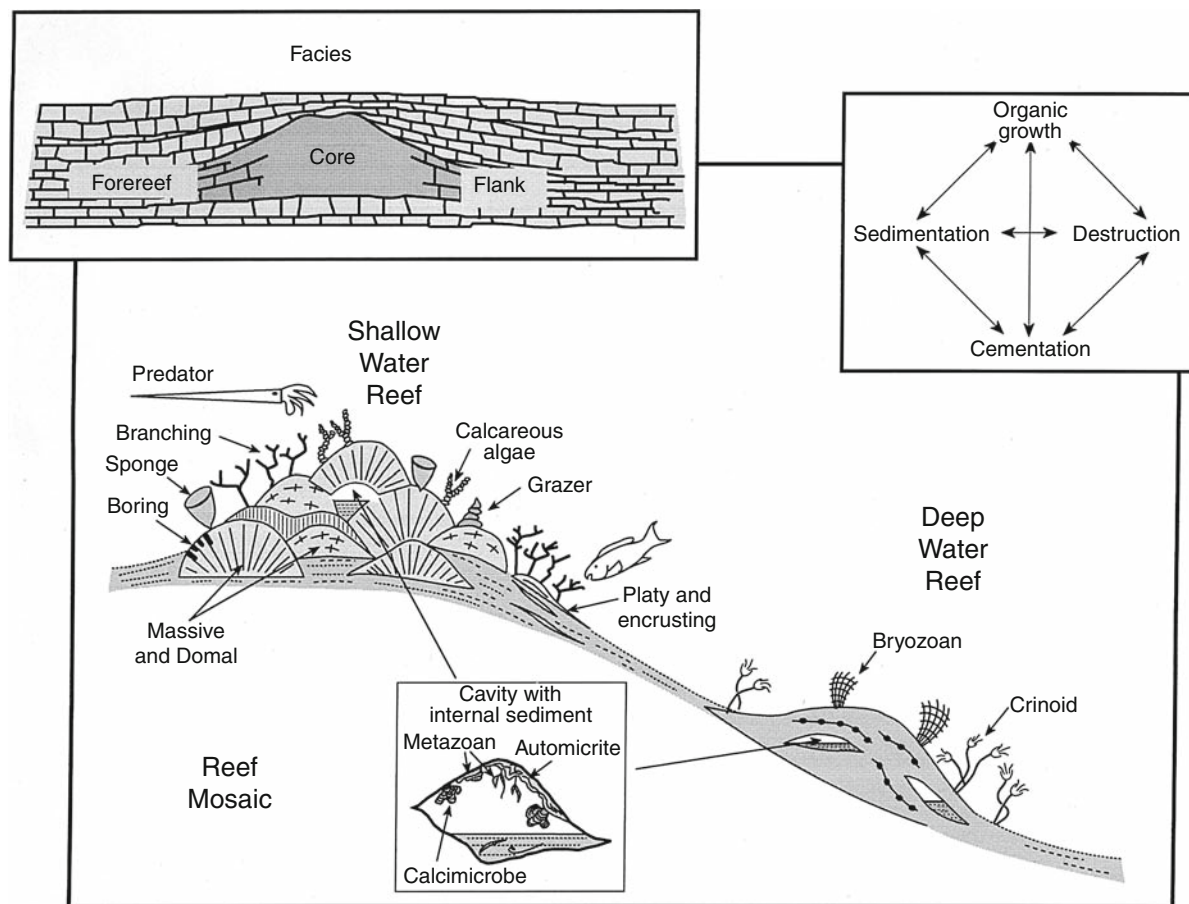
Calcareous metazoans, algae, and microbes can either individually or in combination form a reef. The relative importance and abundance of each has changed through geologic time, leading to the wide array of ancient reef fabrics present in the geological record.

### Calcareous metazoans

All invertebrate taxa of calcareous metazoans have formed reefs at some stage in the past, but the most important groups are sponges, corals, bryozoans, and bivalves. Reef metazoans are often colonial or clonal and are capable of



**General Evolution of Carbonate Reefs, Figure 1** (a) An extensive ancient fringing reef complex: the Permian Capitan Reef, Texas, USA. (b) Isolated patch reef, late Carboniferous (Pennsylvanian), Sacramento Mountains, New Mexico, USA. Field of view = 2 m.



**General Evolution of Carbonate Reefs, Figure 2** A series of sketches illustrating (a) Cross-sectional geometry of a typical reef as exposed in outcrop. (b) Complexity of interrelationships between processes that control reef composition. (c) Main attributes of shallow-water reefs and deep-water mounds. (From James and Wood, 2010.)

surviving and regrowing or even multiplying after damage to their living tissues. All are obligate calcifiers in that the organism controls biomineralization.

Reef calcareous metazoans can be either heterotrophs or mixotrophs. Heterotrophs consume other organisms whereas mixotrophs are heterotrophs that also contain symbiotic microorganisms, generally photosynthetic cyanobacteria or single-celled algae.

Sponges including hexactinellids with siliceous spicules alone and those with calcareous skeletons were major reef builders in the past. Calcified sponges belong to several different groups including calcareans, demosponges, stromatoporoids (a group of sponges of probably mixed affinity that are distantly related to various modern calcified sponges), archaeocyaths, and chaetetids. Corals comprise both tabulates and rugosans from the Cambrian/Ordovician to the end Permian and scleractinians from the mid-Triassic onward. The other important organisms are bryozoans that, even though relatively small and delicate, are critical elements of many reefs and often act as scaffolds between which in situ microbially induced lime mud (micrite) can form and cements precipitate.

Although we cannot be certain about the physiological tolerances of many ancient fossil reef builders, some generalities are possible. In contrast to those organisms that contained phototrophic symbionts, heterotrophs would have been limited by the availability of light and nutrients. On the basis of isotopic (Stanley and Swart, 1995), and growth-form evidence, scleractinian corals probably possessed zooxanthellae by the late Triassic. Tabulate corals were a diverse group of organisms and it is not clear whether they contained similar symbionts. Rudist bivalves formed low-relief aggregations and were massive producers of sediment in the Cretaceous, but some of the most important groups did not appear to have symbionts (Steuber, 1999). Fossil sponges, both spiculate and soft bodied, and calcified sponges (such as stromatoporoids and archaeocyaths) are poorly understood and their association with photosymbionts is uncertain (Wood, 1999).

#### Calcareous algae

Calcareous algae, both red (coralline and squamaracean) and green (codiacean and udoteacean), are obligate

calcifiers. They can form reefs as well as binding and stabilizing reef frameworks being prolific producers of sediment. Such algae probably occupied these niches in the past. Calcareous algae have been part of the carbonate factory since the Ordovician but were not significant in reef communities until the early Carboniferous (Mississippian). Phylloid (leaf-like) algae were conspicuous reef builders in the late Palaeozoic.

### Microbes

Microbes are highly diverse single-celled prokaryotes and eukaryotes. Carbonate precipitation associated with them can be inferred by the presence of often encrusting microcrystalline micrite (lime mud) with peloidal, clotted or laminated fabrics, or by calcified microbial sheaths (calcimicrobes).

Microbes are non-obligate calcifiers in that they induce carbonate precipitation by their metabolic processes or postmortem chemistry: they are incapable of calcification under unfavorable conditions such as low carbonate saturation. The attributes of microbial textures are therefore thought to depend upon seawater carbonate saturation and postmortem preservation.

Calcification often takes place associated with a biofilm consisting of layers of organic matter (EPS – extracellular polysaccharide) that contains a variety of living and dead microbial communities within a matrix of degrading organic matter and mucilage. The precipitated microcrystalline micrite is sometimes called automicrite because it is produced in-place, generally on a substrate, and it can be an important binding or cementing agent.

It is also possible that some micrite formation in reefs relies mainly on early diagenetic organomineralization processes to aid calcite nucleation on dead organic matter, particularly via molecules derived from decayed sponges. The presence of abundant, reactive  $\text{Ca}^{2+}$ -binding fulvic acids have been confirmed in well-preserved Cretaceous mud mounds and modern coral reef caves.

Automicrite is the main constructor of layered stromatolites and clotted thrombolites. Stromatolites, composed of automicrite and symsedimentary cement, were the only reef builders throughout the Precambrian and were augmented by thrombolites and calcimicrobes in the Neoproterozoic. They have continued to be a variable contributor to reefs throughout the Phanerozoic. Calcimicrobes, once established in the Neoproterozoic, have continued to be a significant and sometimes dominant element of reefs throughout the Phanerozoic, particularly the Palaeozoic. Whereas automicrite is essentially an encrusting or binding element in most reefs, often within cavities, it may nevertheless contribute substantially to the reef rock volume.

The most common calcimicrobes are tubular (*Girvanella*, *Rothpletzella*), subspherical (*Renalcis*), or branching (*Epiphyton*). They are generally interpreted as sheaths of bacteria that have undergone variably taphonomic alteration. Many other similar structures of

complex affinity such as the Mesozoic *Tubiphytes* (probably a foraminifer–cyanobacteria association) have also been placed in this category. Calcimicrobes were also important sediment producers.

### Internal cavity systems

Much of most modern and ancient reefs are void space as metazoan-algal-microbe growth geometries often produce interconnected cavities, even in those reefs almost wholly composed of mud. These cavities are often shaded from light and suffer less predation or grazing and reduced wave energy compared to the open reef surface. Cavities are often populated by cryptic organisms that encrust walls and hang down from ceilings. They range from photic organisms near the openings to relatively fragile heterotrophs in the dark, lightless interiors. Automicrite often preferentially coats inner surfaces of cavities and encrusts the cryptic community. Cavities are also sites of fine-grained sediment accumulation, material composed of skeletal debris and mud that forms a geopetal internal sediment fill. Reef cavities first appeared in the Neoproterozoic coincident with calcimicrobes and thrombolites. Thereafter, they were a significant element of most reefs.

### Symsedimentary lithification

Most reefs are lithified immediately below the living surface by a variety of calcareous precipitates. Much of such cement is microcrystalline but other cements are spectacular, growing as millimeter or centimeter-sized crystal arrays from the walls and ceilings of cavities or between sediment grains. Such cements not only confer rigidity to reefs but also occlude much original pore space.

The location of the reef determines the amount of cementation. Platform-margin and down-slope reefs usually contain marine cements, particularly in high-energy areas, whereas lagoonal or inner-ramp reefs rarely do and so may be unlithified.

Symsedimentary cementation is an attribute of reefs of all ages but the type and mineralogy is controlled in part by changing seawater chemistry. The most intensive ancient cementation documented is found in Precambrian reefs, where some are volumetrically dominated by cements. The amount of crystalline cement in reefs decreases with the appearance of calcareous organisms in the Cambrian and then again following the evolution of calcareous plankton in the Jurassic: Many Palaeozoic reefs contain conspicuously more symsedimentary cement than Jurassic and younger examples.

### Bioerosion and predation

Living calcareous reef builders and reef rock are grazed upon by a variety of bioeroders, particularly limpets, echinoids, and fish that not only consume soft parts but also remove reef carbonate, which is reduced to fine sediment. Although present in the Palaeozoic, this component of in-place reef removal, bioerosion, and sediment production



began in earnest in the Mesozoic and has increased dramatically ever since (see entry *Bioerosion*).

### Geologic history of reefs

The Phanerozoic witnessed major turnovers of reef biotas, mass and minor extinction events, and profound changes in the chemistry of seawater. The evolving history of reefs has been reviewed extensively by Fagerstrom (1987), Wood (1999), Stanley (2001), Kiessling et al. (2002), and James and Wood (2010), and is summarized in Figure 3.

Reefs have broadly evolved from dense, stromatolite-dominated reefs of the Archean, with the appearance of thrombolites and calcimicrobes in the Neoproterozoic, forming the first reef cavities, to the successive rise of various skeletal metazoans from the earliest Phanerozoic onward.

During geological periods when large calcareous skeletal and microbial structures were common, reefs grew as fringing reefs landward, as patch reefs across platforms, and as barrier reefs along platform margins. Coeval mounds developed in either quiet water settings across the platform, or on ramps, or on the slope.

The formation of large, shallow-water, flat-topped platforms coincide with the periods of skeletal reef development because skeletal reefs are characterized by well-cemented carbonate buttresses along their seaward margin. These ramparts absorbed waves and swells, thus allowing more tranquil, protected lagoonal facies to develop across the platform interiors. When skeletal reefs were absent, carbonate ramps were the norm, where reef mounds and mud mounds were the only buildups, which either grew leeward of sand shoals or more commonly on deep-water ramps and slopes.

The great diversity of ancient reefs present a continuum of shared ecologies and sedimentary characteristics, but they can be divided into the broad end members of (1) skeletal reefs, (2) skeletal–microbial reefs, (3) microbial reefs, and (4) mud mounds (James and Wood, 2010; Figure 4).

### Skeletal reefs

#### *Shallow reefs*

Skeletal, shallow reefs, where skeletons dominate most of the rock volume, are restricted in geologic time to the (1) middle Ordovician to late Devonian, (2) late Jurassic, and (3) Cenozoic.

Although symsedimentary cements, microbes, and automicrite were present, they are usually of subsidiary importance, except during the intervals of the Palaeozoic. Internal cavities, which may comprise as much as 30% of the reef volume, can be sites of diverse cryptic communities, calcimicrobial growth, and internal sediment. Automicrite is present on, around, and between skeletons. Symsedimentary cement can be spectacular, with the largest amounts found in the reefs at the platform margin. Such reefs were built by calcified sponges (stromatoporoids), tabulate corals, or scleractinian corals.

These reefs, with their large skeletons and relatively rapid growth rates, are amongst the most extensive in the

rock record. Diversity is lowest in reef crest and deep-water environments, with both environments favoring sheet-like skeletal morphologies. The highest diversity of skeletons and shapes, and therefore rock types, occur at intermediate depths.

Growth forms and skeletal diversity are strongly controlled by hydrodynamic energy. Unlike modern corals, Palaeozoic stromatoporoid sponges and tabulate corals, even though they often grew as laminar forms, sat on or were anchored within the sediment (Figure 5). Large, tabular forms that were solidly rooted in the sediment inhabited high-energy zones such as the reef crest, but since stromatoporoids did not typically have an encrusting habit, it is doubtful that they were successful builders in the surf zone. Tabular stromatoporoids, locally bound together by calcimicrobes, automicrite, or cement, are also known to have occurred in energetic waters. Domal, bulbous, and dendroid forms occupied quiet water zones, either below wave base or in sheltered areas of the back reef and the lagoon (such as delicate stick-like amphiporoids). These skeletons were locally reworked during storms and redeposited as rubble units associated with peritidal settings.

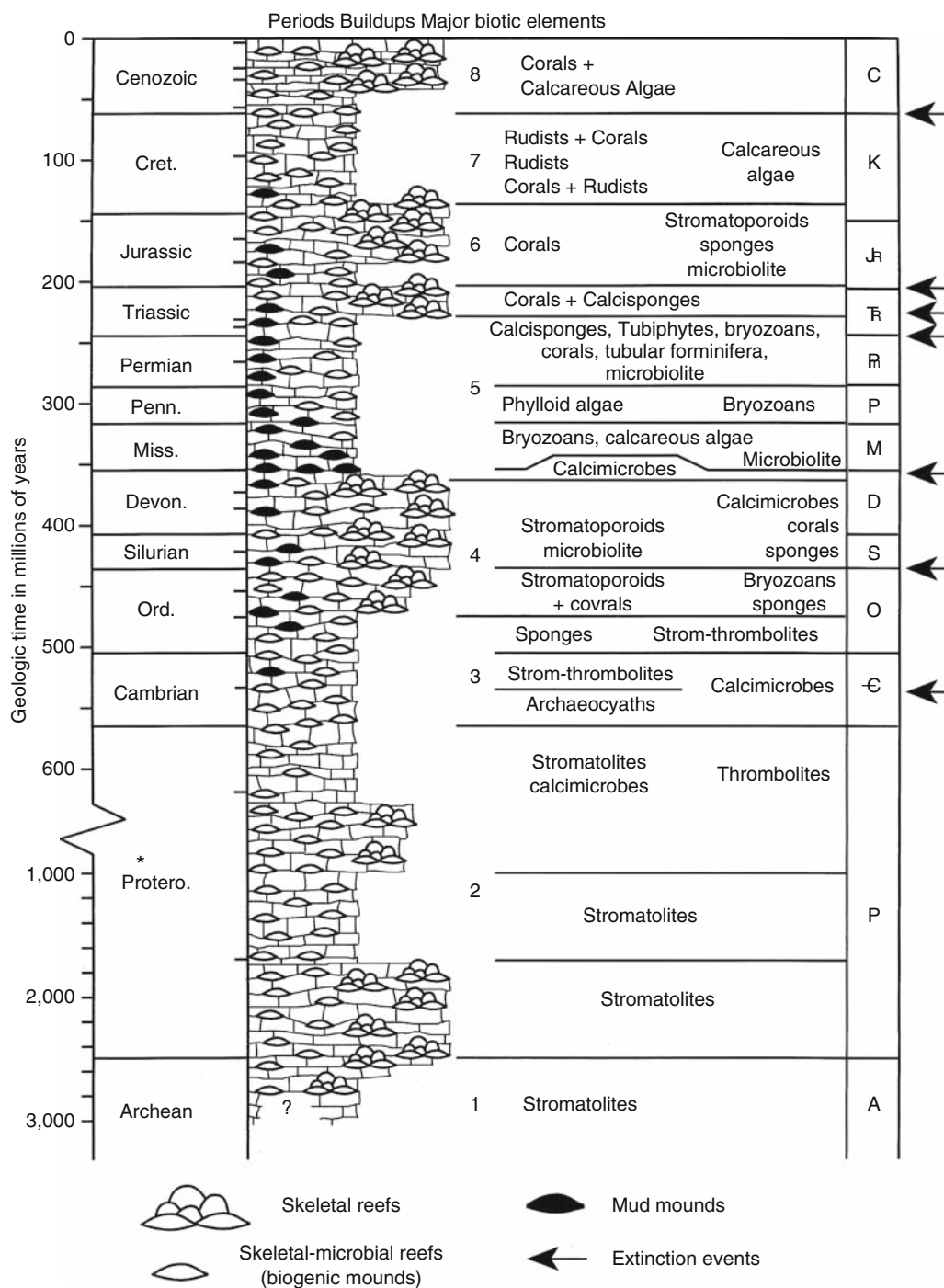
#### *Deep-water skeletal reefs*

Today, deep-water skeletal reefs grow worldwide in water depths of between 250 and 1,500 m, where temperatures range from 4°C to 12°C (Freiwald and Roberts, 2005). They are constructed by scleractinian corals that lack photosymbionts, especially the branching form *Lophelia pertusa*. These reefs are muddy and unlithified and range up to 5 km long and 40 m high, with generally steep sides up to 160 m thick. Many are located in areas of elevated nutrients such as oceanic fronts or upwelling; others are sited on the top of cold hydrocarbon seeps.

Cold-seep reefs are part of a lineage of similar structures that extends back to the Silurian, but there are very few corals from methane seep communities older than the late Eocene. The rock record of such skeletal reefs is not extensive. The oldest known is Triassic, but they are not numerous until the Cenozoic, where an especially good record exists in north-west Europe and the Mediterranean region. Pre-Cenozoic deep-water reefs seem to be either skeletal–microbial mounds or mud mounds.

### Mixed skeletal–microbial reefs

Many ancient reefs bear two important constituents: small or delicate skeletal metazoans that are either heterotrophs or autotrophs (e.g., phylloid algae) and a microbial component of calcimicrobes or inferred microbialite (Webb, 1996; Wood, 1999). These structures with a mixed consortium of organisms are unlike most modern skeletal reefs and have been called reef mounds or biogenic mounds (James and Bourque, 1992). Such reefs often contain extensive framework cavities, with their own distinctive cryptic biotas and abundant symsedimentary cements (Figure 6b).

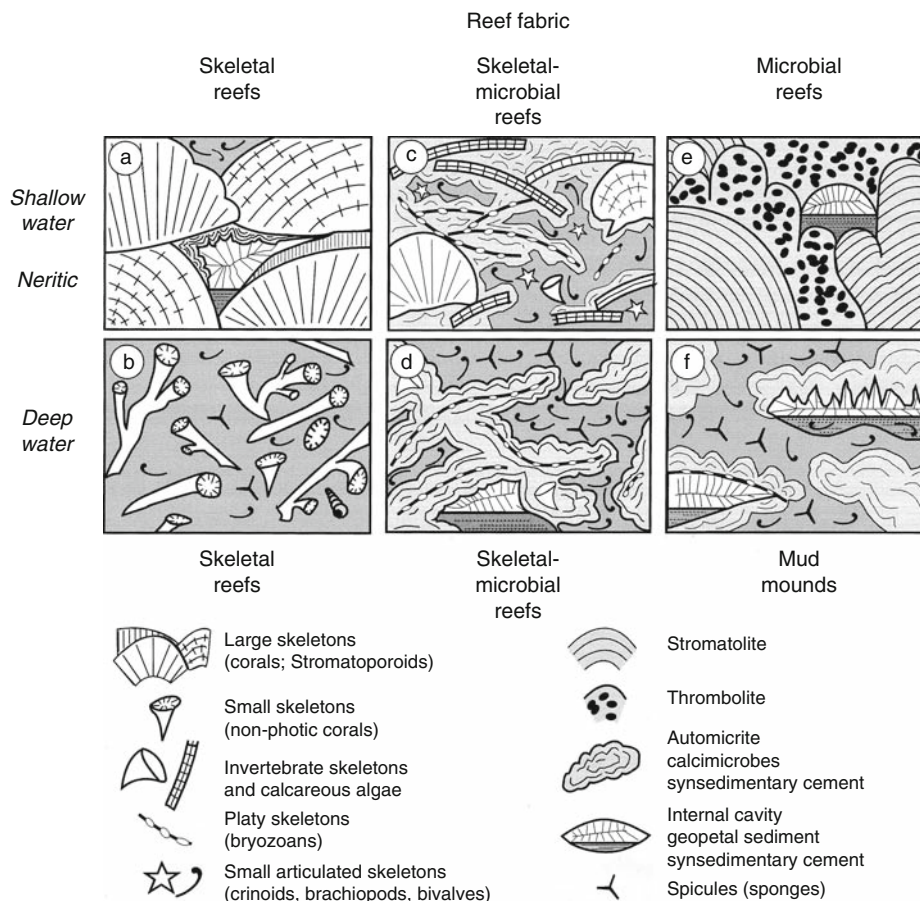


**General Evolution of Carbonate Reefs, Figure 3** Reefs through time, illustrating periods when skeletal, skeletal-microbial reefs, and mud mounds were important. Numbers indicate different associations of reef- and mound-building biota. Arrows – signal major extinction events. \* – scale change. (From James and Wood, 2010.)

Autotroph-microbial or heterotrophic-microbial communities dominated ancient mixed reefs in shallow waters of the photic zone. No direct modern analogs are known for either of these systems.

#### *Autotroph dominated*

Ancient examples of mixed autotroph reefs include Pennsylvanian to early Permian phylloid algal mounds. These algae are probably of mixed affinities and grew as laminar,



**General Evolution of Carbonate Reefs, Figure 4** A modified classification to describe reef carbonates. (From James and Wood, 2010, after Embry and Klovan, 1971.)

cup-, bowl-, or upright leaf-like forms that may have been encrusted by automicrite. Such reefs are usually low-relief isolated structures, appear to have grown in shallow waters, and are often associated with grainy sediments that indicate growth under fairly energetic conditions with extensive flanking beds. These mounds were typically the source of significant skeletal debris that formed extensive flank beds. *Halimeda* mounds have been reported from the late Miocene and may have been stabilized by the rapid lithification of micrite and microbial crusts (Martín et al., 1997).

#### *Heterotroph dominated*

Heterotroph reefs are common in the ancient record. Lower Cambrian reefs occur as small isolated mounds, consisting of archaeocyath sponges and calcimicrobes, particularly *Renalcis* and *Epiphyton* (Figure 7a and b). Lower Ordovician reefs were likewise dominated by calcimicrobes, microbialite and, locally, corals.

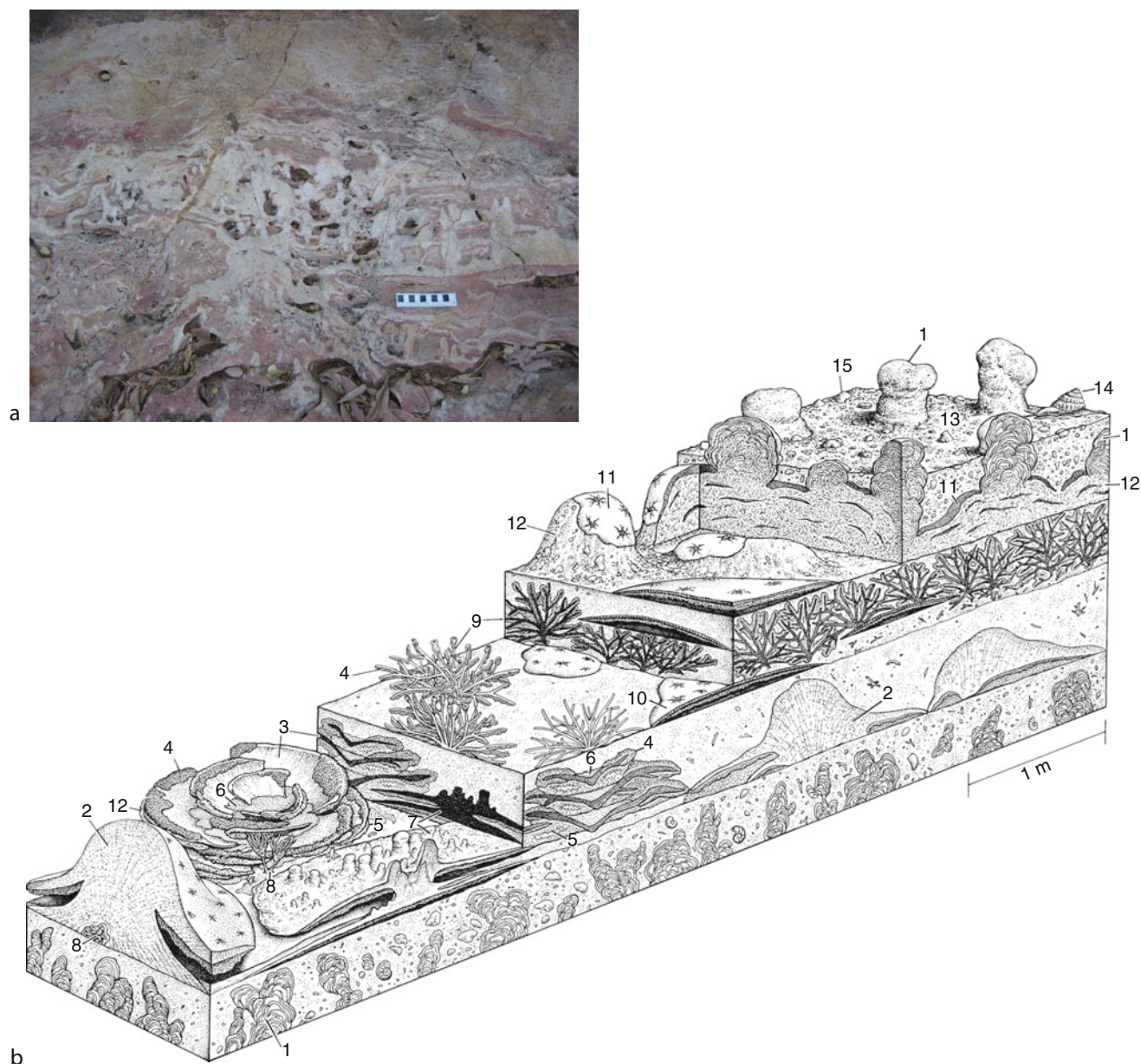
Some back-reef shallow-water Frasnian (late Devonian) reefs exhibit large skeletal metazoans (particularly stromatopore sponges and subsidiary corals), as well

as extensive fenestral microbialite and calcimicrobes, both as free-standing mounds and as secondary encrustations within cryptic habitats (Figures 5b and 6a).

Shallow-water Lower Carboniferous (Mississippian) reefs are formed by endemic communities composed of laminated microbial mounds with a rich encrusting open surface and cryptic fauna dominated by algae, bryozoans, corals, and sponges (Mundy, 1994; Webb, 1994; Ahr et al., 2003).

The mid-to-late Permian is characterized by extensive fringing reefs with a well-developed zonation. They consist in part of a primary framework of frondose bryozoans and calcified sponges (many of whom were cavity dwellers) that were bound by extensive crusts of laminated automicrite (Figure 6b). *Tubiphytes* is common, together with various encrusting algae including *Archeolithoporella*. Volumetrically, many of these reefs were dominated by sediment and syndimentary cement, or automicrite. Such successions are inferred to have formed within open cavity systems with freely circulating seawater, in response to decreasing light and energy conditions as the reef was progressively buried. Upper Jurassic





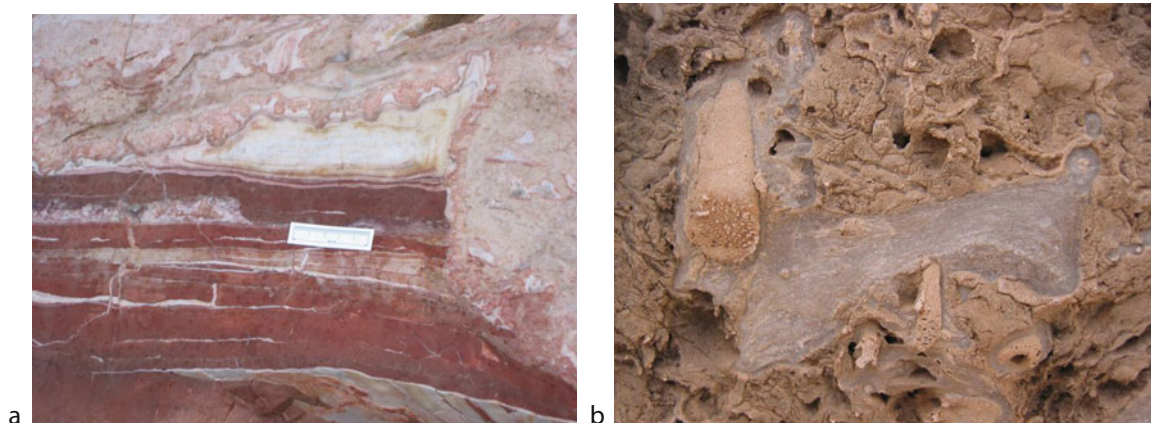
**General Evolution of Carbonate Reefs, Figure 5** (a) Large stromatoporoid sponge, growing over soft sediment. Late Devonian (Frasnian) Windjana Gorge, Canning Basin, Western Australia; scale = 10 cm. (b) Reconstruction of back-reef community, Late Devonian (Frasnian) Windjana Gorge, Canning Basin, Western Australia. 1. Stromatolites, 2. Domal stromatoporoid, 3. foliaceous stromatoporoid, 4. *Renalcis*, 5. fibrous cement, 6. internal sediment, 7. platy stromatoporoid, 8. crinoids, 9. branching stromatoporoid, 10. laminar stromatoporoid, 11. encrusting stromatoporoid, 12. microbialite, 13. clastic sediment, 14. gastropods, 15. Oncolites. (From Wood, 1999; Copyright J. Sibbick.)

shallow-water reefs were dominated by hexactinellid and lithistid spiculate sponges, coated by automicrite and thrombolites, and encrusted by a variety of biota.

#### Deep-water skeletal-microbial reefs

Deep-water, heterotroph-mixed skeletal-microbial reef communities are known from the Silurian to Devonian, Jurassic, and Cretaceous. They were very different from

modern skeletal deep-water reefs. Muddy reefs with *Stromatactis* (Figure 8), lithistid sponges, and calcimicrobes were widespread during the Silurian, and typically show a vertical zonation that culminates in shallow-water stromatoporoid sponge-rich communities. Similar communities, with the addition of microbialites, stromatolites, and receptaculitids, formed deep-water reefs in the mid-to-late Devonian.



**General Evolution of Carbonate Reefs, Figure 6** (a) Late Devonian (Frasnian) reef, showing a large branching stromatoporoid sponge, encrusted by microbialite and *Renalcis*. Cavities are filled with syndeposimentary sediment and cement. Windjana Gorge, Canning Basin, Western Australia; scale = 5 cm. (b) Pendent sponges growing downward attached to a bryozoan frond. The whole framework has been encrusted with microbialite. Remaining cavity space is filled with syndeposimentary cement botryoids. Permian Capitan Reef, McKittick Canyon, Guadalupe Mountains, Texas, USA. Field of view = 6 cm.

Upper Jurassic deep-water mixed reefs were constructed by thrombolitic–stromatolitic columns or mounds associated with *Tubiphytes*, the worm *Terebella*, and hexactinellid and lithistid sponges. The platy scleractinian coral *Microsolena*, which is thought to have fed in part heterotrophically, is found in low-light settings, such as shallow turbid or deep-water environments.

### Microbial reefs

Modern stromatolites are relatively rare and appear to grow in areas of abundant calcium carbonate saturation and where faster-growing algae and seaweeds are excluded due to some environmental stress such as active tidal currents, low nutrients, or high salinity (Figure 9b).

Microbial reefs dominated much of earth history, from the Archean until Middle Ordovician, but they are only found in younger Phanerozoic facies, where most invertebrates have been excluded by environmental stresses. They are built primarily by stromatolites and thrombolites that have a wide variety of morphologies. Precambrian reefs throughout the Archean, early, and middle Proterozoic are essentially a series of stacked stromatolites and, to a lesser extent, thrombolites (Grotzinger and James, 2000). They have neither cavities nor inter-microbial syndeposimentary cements but exhibit a wide variety of delicate branching, lamellar, hemispherical, and conical morphologies that are thought to be due to a combination of different microbial communities, hydrodynamics, and sedimentation rates. These microbialites range in size from centimeter to decimeter, with some large structures up to 8 m high and 30 m long.

Shallow-water, high-energy Proterozoic buildups were formed by isolated stromatolitic domes, linked domes, columnar stromatolites, and their elongate equivalents. Stromatolite fragments were ripped off during storms and deposited as cross-bedded gravels locally surrounded

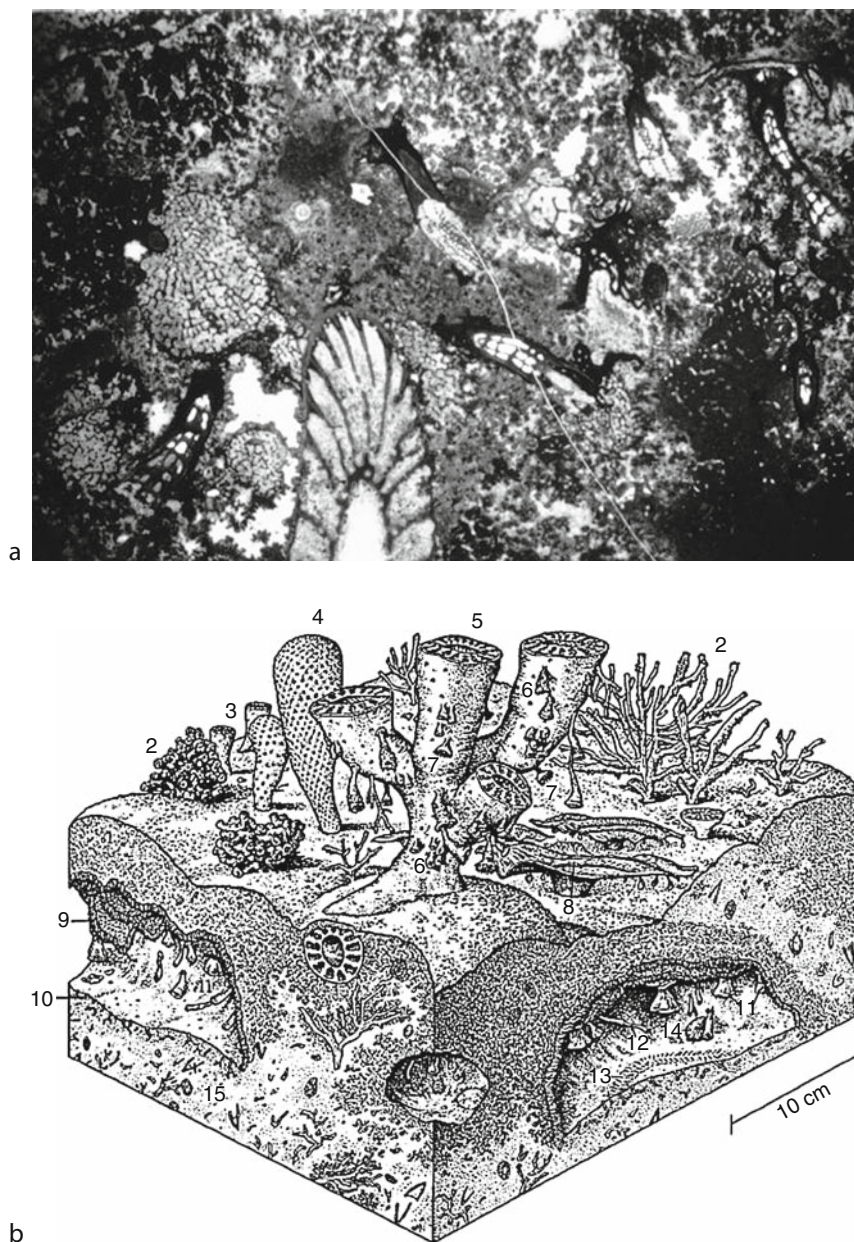
by individual shallow reefs. Reefs at platform margins show a strong zonation of microbialite growth forms that mimic facies zonations of metazoan reefs. Isolated deep subtidal and slope reefs (probably below fairweather wave base) were built primarily by conical stromatolites.

There seems to be an evolution of microbial structures through the Precambrian. Archean and Palaeoproterozoic reefs were mainly syndeposimentary precipitates (possibly microbially mediated) with microbial layers. Microbes appear to become more prominent in Paleoproterozoic and Mesoproterozoic structures. A profound change, however, took place in the Neoproterozoic with the increased importance of thrombolites and the appearance of calcimicrobes as reef builders (Figure 9a). This resulted in the earliest formation of cavities complete with internal sediment and syndeposimentary cement, features that would become a prominent attribute of all subsequent Phanerozoic reefs. This community had the ability to construct reefs with up to 100 m of relief above the sea floor in deeper water environments (Turner et al., 1997). Toward the end of the Neoproterozoic, the first skeletal invertebrates (e.g., *Cloudina*, *Namacalathus*, and *Namapoikia*) began to populate the surfaces of these reefs and were entombed by the microbial precipitates.

### Mud mounds

Mud mounds can form large, often over 100-m high and 400-m wide, isolated, steep-sided structures that consist of more than 80% of a fine-grained carbonate (micrite) (Figure 8b). This micrite has both in situ and detrital origin but often shows accretionary structures constructed by successive phases, known as polygenetic muds (“polymuds”), which form on open surfaces and within semi-enclosed cavities (Monty et al., 1995). Such polymud fabrics produce complex, three-dimensional accumulations that in turn form open frameworks that





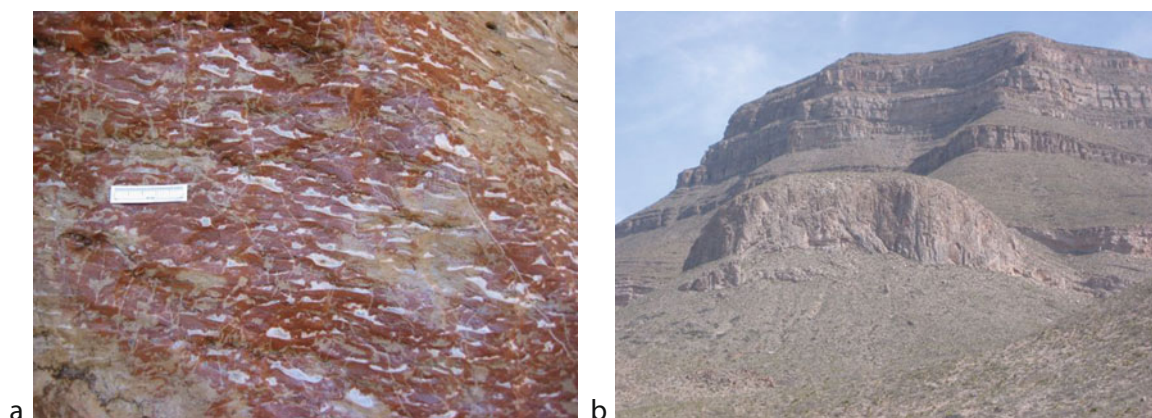
**General Evolution of Carbonate Reefs, Figure 7** (a) Growth cavity in archaeocyath skeletal-microbial reef mound. The cavity is formed by the calcimicrobe *Renalcis* and populated by pendent, solitary archaeocyaths. Lower Cambrian, Siberia, Russia; scale = 5 mm. (b) Reconstruction of lower cambrian archaeocyath community. 1. *Renalcis*, 2. branching archaeocyath sponges, 3. solitary cup-shaped archaeocyath sponges, 4. chancelloriid, 5. radiocyaths, 6. small archaeocyath sponges, 7. "coralomorphs," 8. large archaeocyath, 9. fibrous cement, 10. microburrows, 11. cryptic archaeocyaths, 12. cribricyaths, 13. trilobite trackway, 14. cement, 15. internal sediment. (From Wood, 1999; Copyright J. Sibbick.)

may subsequently be filled with mud or syndimentary cement. Many mounds also display a rich attached metazoan biota of crinoids, tabulate corals, brachiopods, trilobites, sponges, ostracodes, and bryozoans.

The clotted, peloidal or laminated textures, and the encrusting or frame-forming habit argue for an *in situ* microbial or organomineralic origin, augmented by a rapid

syndimentary lithification. This origin is supported by moderate rates of carbonate accumulation (0.2–0.8 m/1,000 years), and the steepness (35–40°) of mound flanks. Abundant *Stromatolites* cavities that parallel the accretionary mound surfaces (Figure 8a) suggest a close relationship between mound formation and internal sediment filled voids, cementation, and carbonate production (Monty et al., 1995).





**General Evolution of Carbonate Reefs, Figure 8** (a) Irregular masses of calcite (*Stromatactis*) that were originally internal cavities partly filled with internal sediment and then occluded by syndimentary cement in a late Devonian (Famennian), Windjana Gorge, Canning Basin, Western Australia; scale = 5 cm. (b) Muleshoe Mud Mound, Mississippian, Sacramento Mountains, New Mexico, USA.



**General Evolution of Carbonate Reefs, Figure 9** (a) Neoproterozoic thrombolites, Nama Basin, Namibia. (b) Living stromatolites in Shark Bay, Western Australia.

Mud mounds were often established in deep waters below the photic zone as indicated by the absence of algae and cyanobacterial activity. Locally, however, they show shallowing-upward facies signatures, characteristic of shallow depths and significant depositional energies. In the Frasnian “*récifs rouges*” of the Belgian Ardennes, the basal facies is composed of *Stromatactis*-rich red lime mudstone to wackestone with abundant sponge spicules. This may have formed in hypoxic waters below the photic zone. Platy corals appear higher but are overlain by a more diversified coral, stromatoporoid, and skeletal algae wackestone to packstone with *Stromatactis*. Uppermost facies consist of a stromatoporoid, coral, and bryozoan framework with various microbial and calcimicrobial encrusters, which formed in photic waters above fair-weather base and sometimes in restricted or lagoonal environments.

Early Mississippian reefs (Waulsortian facies) also show a similar progression of facies. The growth of the

well-known Muleshoe Mound in New Mexico (Figure 8b) records a shift from predominantly upward (aggradational) to lateral (progradational) growth. The largest volume of these buildups is composed of polymud fabrics with early cements, sponges, and large fenestrate bryozoans. The framework is composed of rigid micrite masses with rounded, bulbous shapes, and thrombotic fabrics that are lined by early marine cements. In the uppermost facies, both the microbialites and large bryozoans grew with a pronounced high-angle orientation into currents. Crinoid-rich flanking grainstone beds draped the reef slopes. In places, fenestrate bryozoans built a delicate framework that formed a limestone containing up to 90% of early fibrous cement.

The location and initiation of mud-mound formation appears to be mediated by environmental factors that differ from those of shallow skeletal reefs. Indeed, there may therefore be real differences in the style of primary production and organic matter recycling between these

different reef systems. Deep-water mud mounds are commonly found in groups, suggesting that their formation was environmentally mediated. Several environmental triggers have been proposed: the episodic formation of nutrified water masses reduced sediment supply during platform drowning or localized oxygen depletion of seawater. Some mud mounds are aligned along faults or fissures, which may have acted as conduits for hydrothermal fluids. For example, the microspars and brachiopods of Muleshoe mound have been shown to have higher  $\delta^{13}\text{C}$  values than non-mound samples, possibly related to methanogenic fermentation.

Mud-mound formation began in the Palaeoproterozoic (probably Neoproterozoic) and extended until the Miocene, but they are mostly a Palaeozoic phenomenon, with widespread mud-mound formation occurring during the early Cambrian, the lower Ordovician, the late Devonian, and the Mississippian, which was dominated by Waulsortian mounds.

### Origin of the modern coral reef ecosystem

The modern coral reef ecosystem is geologically very young. Scleractinian corals appeared in the mid-Triassic and had almost certainly acquired photosymbionts by the late Triassic at the latest (Stanley and Swart, 1995). The ancestral stock of the modern reef biota appeared in the middle Jurassic but was largely suppressed by the prolific growth of calcitic rudist bivalves in the Cretaceous, only to rebound after the end-Cretaceous extinction. There is considerable debate, however, as to whether this coral-dominated biota was able to construct spectacular large reefs like those of the modern day before the Cenozoic.

Most modern coral genera appeared in the Eocene–Miocene, and many extant species extend back no further than the Pliocene. Modern reef fish appeared in the Eocene, but the oldest record of parrotfish (scarid) remains are from Miocene sediments dated at 14 million years ago (Ma).

During the Oligocene, the compression of climatic belts and the rise of the Isthmus of Panama created two distinct regions of reef growth to the Caribbean and Indo-Pacific. As a probable result of climatic cooling or habitat loss, a major episode of coral faunal turnover ensued between 4 and 1 Ma in the Caribbean (Budd et al., 1994). Extinction of genera in the Pocilloporidae and Agaricidae was most marked, but many of these genera continued to persist in the Indo-Pacific. A similar differential extinction coincident with corals, removed many fish, including all large excavating scarids, herbivorous siganids, and plantivorous caesionids from Atlantic reefs (Bellwood, 1997).

Although acroporid corals appeared in the Eocene, pocilloporids appear to have dominated Caribbean reefs from 5 to 6 Ma, but following a 1-million year (Myr) transition period of mixed acroporid–pocilloporid assemblages, acroporids became dominant in reef communities in the early Pleistocene (approx. 1.6 Ma). Acroporids may not, however, have achieved levels of extreme abundance until the late Pleistocene (approx. 0.5 Ma)

(Budd and Kievan, 1994). With this as yet unexplained rise to dominance of branching *Acropora*, and a corresponding decline in massive, domal corals, coral reef communities with a completely modern aspect appeared about 0.5 Ma. Except for the extinction of *Pocillopora* in the Caribbean at about 60,000 years (ka), the patterns of community membership and dominance of coral species appear to have been highly predictable for at least the past 125,000 years (Kyr) (Pandolfi and Jackson, 2001).

### Response to long-term environmental change

Climate and changing seawater chemistry are important controls on the history of reef growth, in terms of both complex feedback mechanisms that govern skeletal mineralogy and hence promote some groups over others, and controlling the styles of early lithification.

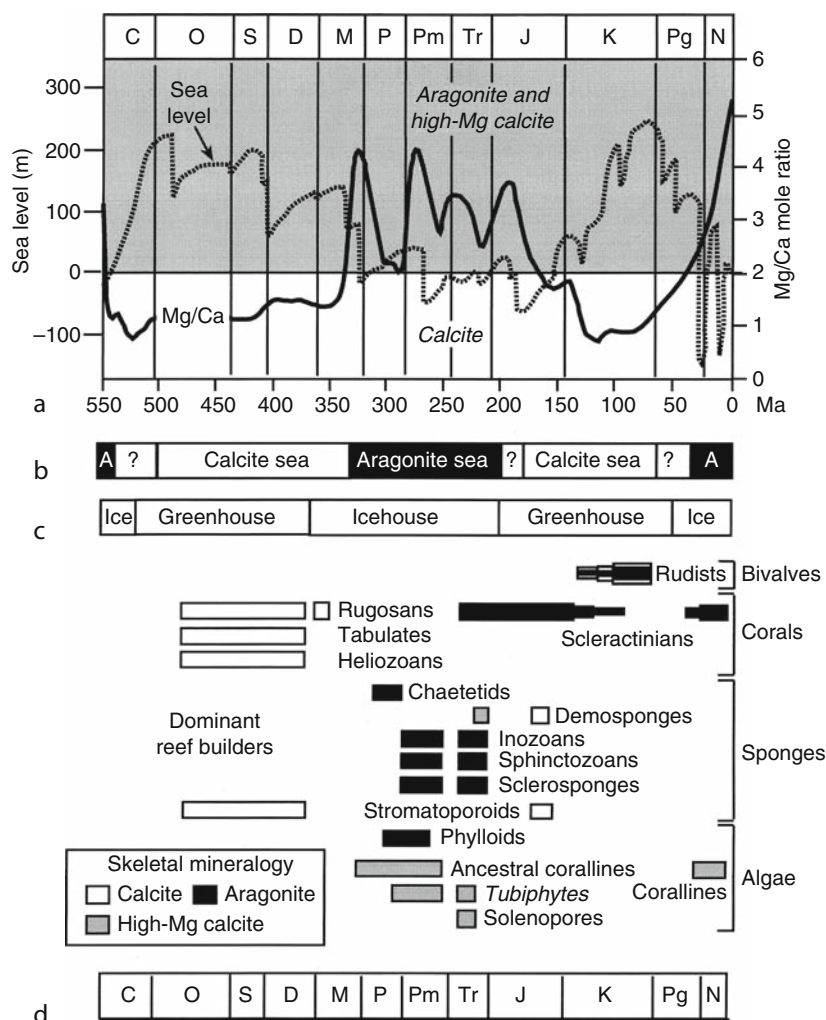
Tectonics ultimately drives many aspects of reef growth such as sea level, circulation patterns, climate, and evolving seawater chemistry change over long timescales (Figure 10). Reefs and carbonate platforms commonly initiate on preexisting highs such as horst blocks or salt domes during the early stages of rifting. Reefs are most numerous on passive continental margins at low latitudes where they typically form barrier or fringing reefs. Similar carbonate shelves with reefs can form around the margins of shallow intracratonic basins, where they can be interbedded with evaporites. Such basins may be prone to isolation from the open ocean, leading to infilling by extensive evaporites.

Rates of thermal subsistence on passive margins are slow and predictable and are similar to those found in intracratonic basins. Reef geometries are thus generally compound to progradational. By contrast, reef-forming toward the cratonward side of foreland basins is relatively rapid and reef geometries more aggradational. Finally, reefs forming in strike-slip basins and on thrust complexes are affected by the vagaries of local tectonic movements, which may be highly episodic but involve substantial displacements and are thus highly unpredictable.

Epeiric seas, those that formed by the extensive flooding of continents during globally high sea levels, have negligible basin floor topography. Water depths rarely exceeded 10 m, such that shallow subtidal and intertidal sediments dominate, with many episodes of exposure. Epeiric seas could support patch reefs, often elongated because of wind waves, storms, or tides. Due to the limited accommodation space on epeiric platforms, progradation is the dominant depositional process, resulting in stacked shallowing-upward sequences or biostromes.

### Climate

Climate is a major controlling force on the evolution of reefs on both short and long timescales, as the latitudinal range of carbonate-producing species is largely governed by temperature and carbonate supersaturation. Reef growth therefore shows cyclicity at all scales in response to short-term



**General Evolution of Carbonate Reefs, Figure 10** (a) Correspondence between changing ocean chemistry and carbonate mineralogy through time as a function of the Mg/Ca mole ratio in seawater (Stanley and Hardie, 1998) and general global sea-level change (Vail et al., 1977); the boundary between the fields of calcite ( $<4$  mole%  $\text{MgCO}_3$ ), and high-Mg Calcite ( $>4$  mole%  $\text{MgCO}_3$ ) and aragonite is the horizontal line at  $\text{Mg/Ca} = 2$ ; (b) the different dominant nonskeletal mineralogies precipitated in seawater through time (Sandberg, 1983); (c) the different global climatic and oceanographic periods (Fischer, 1982); (d) mineralogy of different reef-building organisms (Stanley and Hardie, 1998). (From James and Wood, 2010.)

oscillations (e.g., Milankovitch and glacial–interglacial cycles) as well as to longer-term climatic intervals driven by slower, tectonically driven processes.

Global climate has oscillated through greenhouse and icehouse phases, in concert with aragonite and calcite seas, respectively (Figure 10). During icehouse times of continental glaciation (e.g., Pennsylvanian–early Permian, Miocene–Pleistocene), high-frequency sequences on carbonate platforms were generated by eustatic sea-level changes of 50–100 m. Subaerial exposure, unfilled accommodation space, and conspicuous regional disconformities were common. Aggrading reef growth in a keep-up mode is dominant in icehouse times, as rates of production barely match those of accommodation space increase. These large changes in sea level caused ramps

to have steep gradients and platform tops to have significant depositional relief, characterized by pinnacle reefs and erosional topography. Icehouse reefs are typically dominated by heterotrophs or autotrophs with aragonitic or high-Mg mineralogies.

During greenhouse times with little global ice (e.g., late Cambrian–early Ordovician, Devonian, Triassic, Cretaceous), reef sequences were generated by small (possibly  $<10$  m or so) sea-level fluctuations. Reef cycles typically consist of very shallow-water facies, with regional-scale tidal flat caps and minor disconformities. Greenhouse reefs are often either compound or progradational as reef growth could easily match or outpace the fastest rates of sea-level rise. TST reefs, with plenty of accommodation space were continuously in catch-up or keep-up mode, and this part



of the reef is normally the thickest but narrowest. Ramps often have very low gradients and platforms tend to be progradational, with minor topography. Greenhouse reefs can also have a more extensive range as carbonate settings extend into higher latitudes due to elevated global temperatures. Composition may also be more uniform, often dominated by low-Mg calcite skeletal components.

### Carbonate saturation

Living coral reefs are restricted to shallow-water tropical and subtropical environments characterized by warm temperatures, high light intensities, and also high aragonite supersaturation. The growth of coral skeletons and other calcifying organisms precipitates carbonate ions, forcing a re-equilibration of the bicarbonate-dominated marine inorganic carbon system which also creates a source of carbon dioxide. A coral reef therefore represents the net accumulation of  $\text{CaCO}_3$  and a source of  $\text{CO}_2$ , which in turn probably leads to feedback-controls on the global carbon cycle.

Carbonate saturation has probably varied dramatically throughout geological time. It appears that Precambrian oceans were highly oversaturated, but this may have declined around the beginning of the Phanerozoic with the appearance of numerous calcareous invertebrates. Since then,  $\text{Ca}^{2+}$  in seawater has broadly followed sea-level change such that  $\text{Ca}^{2+}$  levels were reasonably high during the Cambrian-Mississippian and the Jurassic to Cretaceous.

It has been suggested that the geological distribution of microbialites might be controlled by physicochemical factors, including the saturation state of seawater and/or global temperature distribution (Webb, 1996). This may also explain the decline in abundance of reef microbialite after the Jurassic due to the increase of pelagic carbonate that led to a reduced seawater saturation state. This would have lowered supersaturation levels below a threshold for abundant automicrite formation, thus restricting its formation to cryptic reef habitats, where abnormal chemistries could have existed. Such a situation might also explain the absence of *Stromatolites* in the late Phanerozoic.

### Evolving ocean chemistry

The dominant form of precipitated crystalline  $\text{CaCO}_3$  has oscillated during the geological past, with both inorganic and organic production of aragonite and high-Mg calcite dominating carbonate formation during cool periods (ice-house), and low-Mg calcite predominating during warm periods (greenhouse) (Figure 10). Such mineralogical shifts are interpreted as markers for major changes in seawater chemistry.

Stanley and Hardie (1998) have proposed that the shifts in the Mg:Ca ratio have controlled the predominance of calcite versus aragonite secretors, particularly reef builders, due to the inhibiting effect of high  $\text{Mg}^{2+}$  concentration on calcite secretion. They suggest that the changing Mg:Ca ratio of seawater has been controlled by variations in the rate of production of oceanic crust, because oceanic hydrothermal alteration is a major sink for Mg and an

important source of Ca. Experimental work has subsequently confirmed the profound influence of Mg:Ca seawater ratios on modern reef builders, including scleractinian corals (Ries et al., 2006) and the calcareous green alga *Halimeda*.

Scleractinian corals were, for example, important reef builders in the Jurassic, but they did not build extensive reefs during the greenhouse period (calcite seas) of the Cretaceous. During this period, species diversity remained high but their abundance on carbonate platforms was low compared to the Jurassic. Distribution shifted to outer platform settings and higher latitudes ( $\sim 35\text{--}45^\circ \text{N}$ ). There are many hypotheses offered to explain these observations, including the high temperatures, restricted circulation, and unstable sediment conditions of Cretaceous platforms, and in particular the favoring of calcite-producing rudist bivalves over aragonite corals (Wood, 1999). Rudist bivalves with their outer calcitic skeletons underwent a dramatic radiation in the late Cretaceous when the Mg:Ca ratio of seawater reached exceptionally low values so favouring calcite over aragonite secretors (Steuber, 2002).

Major shifts in the dominant composition of carbonate skeletal particles through geological time also mirrors in part these proposed changes in seawater chemistry and climate (Figure 10d), but mass extinctions also play a role by triggering changes in the predominant form of  $\text{CaCO}_3$  produced by marine calcifiers (Kiessling et al., 2008). Changes in the abundance of aragonitic organisms following mass extinction events appear to have been predominantly driven by selective recovery rather than selective extinction.

Evidence is also persuasive that the changing seawater chemistry has influenced the style of early diagenesis in carbonate regimes, particularly in reefs. The mineralogy of early marine reef cements also seems to follow the same secular changes. For example, aragonitic botryoids are known exclusively from phases of aragonite seas (early Cambrian, mid-Carboniferous to early Jurassic, and mid-late Cenozoic), whereas radial fibrous calcite is common in reefs that grew in calcite seas (particularly the Ordovician to Devonian); it is virtually unknown from aragonite seas of the Cenozoic. Enhanced rates of calcite cementation during calcite seas due to the elevated abundance of calcium ions may have promoted rapid lithification of the reef framework and aided preservation of cryptic biota that were otherwise vulnerable to disturbance, but this has yet to be documented.

### The rise of predation and bioerosion

Many researchers have summarized the importance of herbivores and large marine vertebrates to the healthy functioning of coral reefs, and this importance is corroborated by analysis of the fossil record (see Wood, 1999, 2002). A dramatic escalation of new organisms with innovative and destructive feeding methods occurred from the mid-Jurassic to Miocene (summarized in Vermeij, 1987). In particular, the arrival of piscine herbivores had

the potential to fundamentally alter the dynamics of reef and other benthic marine communities.

In general, grazers and carnivores throughout the Palaeozoic and early Mesozoic were relatively small individuals with limited foraging ranges incapable of excavating calcareous substrates. A radiation during the Devonian of durophagous, mobile predators has been proposed by Signor and Brett (1984), but these forms probably relied upon manipulation only to crush or ingest (Harper and Skelton, 1993). By the early Mesozoic, sessile organisms had to contend with an increasing battery of novel and more advanced feeding methods as well as sediment disruption due to deep bioturbating activity (see summary in Vermeij, 1987). Most notable was the rise of efficient excavation behaviors.

Bioerosion notably increased in intensity from the mid-to-late Jurassic. A radiation of borers occurred from the Triassic onward, with deep borers (capable of penetration greater than 50 mm) appearing from the Jurassic. Clionid sponges – one of the major bioeroders on modern coral reefs – had become abundant by the latest Jurassic. The first live borers are known from the Eocene (Krumm and Jones, 1993), as are fishes similar to modern reef faunas (Bellwood, 1996). The ability for substantial excavation of hard substrata over large areas increased considerably from the latest Cretaceous-early Tertiary when deep-grazing limpets, camarodont sea urchins, and especially the reef fishes appeared. The complex pharyngeal apparatus of labrids was present at this time, and major labrid clades were already differentiated (Bellwood, 1997). Balistids first appeared in the Oligocene, and the oldest scarid fossil capable of deep excavation currently known

is from the Miocene (14 Ma) (Bellwood and Schulz, 1991). It seems likely that sometime during the Oligocene–Miocene, reef bioerosion gained a modern caste.

The abundance of reef fishes is assumed to be of great importance on coral reefs, as evidenced by the dramatic increase of algal growth as a result of their decline on Jamaican reefs. Tropical marine hard substrata are usually sparsely vegetated, but a rich algal flora develops when herbivorous fish are excluded and/or nutrient input increases. Grazers not only allow the dominance of corals and coralline algae on coral reefs, they also contribute notably to carbonate sediment production and redistribution, algal ridge formation, and the maintenance of overall diversity. Like other predators, they can also ameliorate the effects of competition and may combine with physical controls to produce the characteristic zonation of modern coral reefs.

The response of reefs to predation has been reviewed by Wood (2002, in press). Table 1 outlines the major causes and indirect effects of predation, particularly herbivory, on coral reef communities. From this, we might be able to make a series of predictions concerning changes in post-Palaeozoic reef community ecology based on their rise to abundance in the fossil record. In the sections following, these predictions are tested in order to determine to what extent the evolutionary history of reef-bioerosion and bioturbation has been bound with the ecology and taphonomy of reef ecosystems.

### Response to increased biological disturbance

Only skeletal anatomy and morphology, spatial distribution, and skeletal attack or breakage, and regeneration might be detected – or inferred – in the fossil record of

**General Evolution of Carbonate Reefs, Table 1** Predicted changes in reef community ecology and taphonomy based on the rise to abundance of new predatory methods and endoliths as evidenced in the fossil record. (After Wood, 1999, 2002)

| Event                                        | Prediction                                                                                                                    | Timing                              |
|----------------------------------------------|-------------------------------------------------------------------------------------------------------------------------------|-------------------------------------|
| The rise of macroherbivores                  | A shift to more conspicuous, well-defended macroalgae (coralline algae) on reefs                                              | Late Mesozoic-Eocene                |
| The rise of specialized predators            | Increase in diversity and retardation of dominance; reducing or preventing competition                                        | Late Mesozoic-Eocene                |
|                                              | Limiting of foraging ranges                                                                                                   | Late Mesozoic-Eocene                |
| The rise of excavatory grazers and predators | Zonation: interaction of physical controls with differential effects of damselfish in the survival of different coral species | Eocene                              |
|                                              | A shift to organisms with deterrent traits and those that tolerate partial mortality                                          | Late Mesozoic to Miocene            |
|                                              | Increase in multiserial, branching corals                                                                                     | Cretaceous onward                   |
|                                              | Increase in the diversity of the cryptos and other spatial refugia                                                            | Jurassic onward                     |
| Rise of intense bioerosion and endoliths     | Algal ridge formation by coralline algae                                                                                      | Eocene                              |
|                                              | Reduced reef framework preservation                                                                                           | Late Mesozoic to Miocene            |
|                                              | Sediment grain size reduction                                                                                                 | Late Mesozoic to Miocene            |
| The rise of parrotfish                       | An increase in skeletal sediment production                                                                                   | Late Jurassic                       |
|                                              | Increase in multiserial scleractinian corals                                                                                  | Throughout the history of the group |
|                                              | Formation of sediment aprons                                                                                                  | Miocene                             |
|                                              | Thick coralline algal crusts                                                                                                  | Miocene                             |
|                                              | Reduction in rate of reef progradation                                                                                        | Miocene                             |

reef organisms. The appearance of these herbivores paralleled profound changes in reef ecology, including the rise of well-defended, highly tolerant coralline algae (Steneck, 1985), a notable increase in branching corals since the late Cretaceous (Jackson and McKinney, 1991), and the loss of many functional organisms that prove to be intolerant to excavatory attack (Table 1). This suggests a cause–effect system, where adaptation to predatory attack has been intimately bound to the origin and assembly of modern reefs.

#### *Secure attachment to a hard substrate*

Organisms without secure attachment to a stable substrate are susceptible to the effects of all disturbances, including bioturbation, as inversion and burial will cause death. Most modern suspension feeders require a hard substrate, even if these are only isolated patches within areas of unstable, soft substrate.

Possession of an edge zone in all but the most primitive scleractinian corals allows them to gain permanent attachment to a stable substrate. As a result, scleractinian corals dominate modern reef framework environments, especially those in high-energy settings, where there is also an abundance of wave-swept, extensive hard substrata for colonization. Permanent attachment also allows the development of very large branching morphologies.

Cambrian archaeocyath sponges usually bore small holdfasts that enabled limited attachment to hard substrates (Figure 7a). But many mid-to-late Palaeozoic reefs were dominated by large, sheet-like invertebrates (stromatoporoid sponges, tabulate and rugose corals, and trepostome and cystoporoid bryozoans) that were initially attached to small, ephemeral skeletal debris and then grew over the surrounding sediment (Figure 5). Small, branching forms (some stromatoporoids and bryozoans) lacking extensive attachment sites were also common, and they were presumably partially rooted in soft sediment.

The late Paleozoic decline of immobile epifauna coincides with the rise of major bulldozing taxa, which passed through the end-Permian extinction unscathed. This coincidence must remain conjectural until tested experimentally.

#### *Resistance to partial mortality*

Predation that actively excavates underlying skeleton often results only in partial mortality, that is, sublethal damage. In such cases, the capacity of the prey to heal or replace damaged areas of soft tissue becomes critical to survival. Strategies that rely upon herbivores/predators to remove competing algae therefore often entail the loss of the prey's own tissues.

In coralline algae, a protective outer epithallus and conceptacles that contain reproductive structures have been demonstrated to protect the delicate reproductive anatomy from intensive grazing (Steneck, 1982). Many coralline algae can also tolerate intense herbivory due to their ability to rapidly regenerate removed material. Thickened

crusts are more tolerant to attack than thin encrusting or branching forms (Steneck, 1985), but in modern reefs, the dominance of a particular growth form appears to be a trade-off between the cost of investment in increased defence, and the reduction in growth rate or competitive ability. As a result, thickened crusts dominate only in areas of high wave energy and biological disturbance.

After the Eocene, herbivore-susceptible, delicately branched coralline algae reduced in abundance in the tropics, the proportion of thickened encrusting forms increased, and the first algal ridges appeared – all coincident with the rise of excavatory herbivorous fish.

Many sessile reef organisms possess a modular or colonial habit where partial predation and boring may remove either individual or a few modules, or large areas may be cleared of living tissue, sometimes together with the excavation of underlying skeleton. But the modular organization also reduces soft tissue to a relatively thin veneer over a larger basal skeleton. This not only decreases accessibility and the ease of prey manipulation by predators but also minimizes the tissue biomass while maximizing the cost of collection. For example, in a typical domal colony of *Porites*, only about 0.5% of the colony's radius is occupied by soft tissue (Rosen, 1986). In branching and platy colony forms, the relative proportion of skeleton is even higher.

Cambrian archaeocyath sponges show a steady and marked increase in the proportion of complex modular forms during their history (Wood et al., 1992), as do scleractinian corals since the mid-Triassic, which appears to be uninterrupted by the end-Cretaceous extinction event (Coates and Jackson, 1985).

#### *Regeneration after breakage*

Some morphologies are more resistant to breakage than others. For example, colonies with closely spaced branches can make predator access difficult by forming hidden, protected areas. The flattening of branch terminations can also offer greater resistance to all forms of breakage and shearing, and this character is found in erect species of bryozoans, gorgonian corals and stylasterine corals.

A multiserial modular organization, however, in addition to promoting architectural diversity and flexibility, also allows compartmentalization of damage and enables some colonies to regenerate from fragments. Most significantly, branching corals also show tremendous powers of regeneration: *Acropora palmata* has one of the highest rates recorded. Indeed, unlike massive, platy or encrusting forms, damage to branching corals often leads to an immediate increase in growth rate so causing an increase in size rather than simply repairing damaged tissue. The staghorn coral (*Acropora cervicornis*) is able to re-anchor fragments and rapidly regenerate and grow, often fusing with other colonies. Such branching corals have turned adversity into considerable advantage, and appear to flourish because, and not in spite, of breakage.



The percentage of scleractinian erect species decreased until the late Cretaceous (Turonian), but increased markedly – particularly in multiserial forms with inferred rates of rapid regeneration – after that time. This spectacular rise of various morphologies of branching forms was coincident with the appearance of new groups of predatory excavators.

All families of modern scleractinian corals that dominate reefs today spread throughout the Tethys Sea during the Eocene. The poritids, their relatives the actinids, and the favids (which had survived the Cretaceous extinction) dominate most coral reef communities throughout much of the Cenozoic (McCall et al., 1994). Although branching acroporoids appeared in the Eocene, they did not dominate reefs until early Pleistocene. The rise of this group – with its particularly remarkable powers of regeneration from fragmentation and rapid growth – would then seem to be independent of any known changes in predation style.

#### *Patterns of sediment removal and storage*

Unlike modern reefs, anecdotal evidence suggests that a greater proportion of reef framework is preserved in situ before the Jurassic (Wood, 1999). Many Palaeozoic reefs commonly preserve intact reef frameworks, even of fragile biota such as frondose bryozoans (Figure 6b) or platy stromatoporoid sponges. Such preservation was aided, in part, by abundant and probably rapid syndimentary lithification, particularly cementation.

We might predict that substantial aprons of sediment may not have been present on pre-Eocene reefs before the evolution of reef fish, and likewise in the absence of the grain size reduction activities of clionid sponges, echinoids, fish, mean sediment grain size may have been more coarse prior to the late Jurassic, perhaps resulting in a reduced net loss of carbonate to the system through the removal of fines. It is possible also that the modern style of coral reef lagoon may also not have appeared until the late Jurassic or later (Wood, 1999, 2010).

### **The role of mass extinctions**

Reefs have long been thought to be highly susceptible to mass extinction events, with major reef-building biota typically going largely or wholly extinct. Metazoan reefs may take some 2–8 Myr to recover after such events, sometimes longer than other communities, and post-extinction reefs are often composed of entirely new groups of skeletal metazoans.

In some cases, either calcimicrobes or microbialites can dominate post-extinction reefs, but these elements were often already part of the pre-extinction reef community. Shallow-water Frasnian (late Devonian) reefs show abundant large skeletal metazoans (particularly stromatoporoid sponges, and subsidiary corals) as well as extensive fenestral microbialite and calcimicrobes both as free-standing mounds (Figure 5b). Succeeding Famennian reefs growing in the aftermath of a mass extinction were composed of frame-building microbialite and calcimicrobes (e.g., *Renalcis* and *Rothpletzella*) and a diverse community of

spiculate sponges. The first metazoan reefs to form after the end-Permian extinction in the Anisian (Lower Triassic) bore large framework cavities, populated with the calcified microbe *Cladogirvanella*.

Tropical shallow marine carbonate production has been noted to fall after some mass extinctions (e.g., the late Devonian and end Permian), but not others (end Cretaceous). Changes in seawater saturation or chemistry may also explain the response of reef and other carbonate-producing biota to mass extinctions. When skeletal groups first appear, they tended to adopt the mineralogy favored by ambient seawater chemistry, but subsequent extinction events may have preferentially removed those groups and selected for new skeletal biota whose skeletal mineralogy reflected the new ocean chemistry (Kiessling et al., 2008).

### **Summary**

Reefs have shown some unifying features over their 3.5-billion-year history. Reefs have shown zonation in response to environmental gradients from their inception, and metazoan reefs have been differentiated into open surface and cryptic reef communities for their entire ~550-million-year history (Wood et al., 2002).

Tectonics drives many aspects that control reef growth including sea level, circulation patterns, climate, and evolving seawater chemistry change over long timescales. Reefs have always been most numerous on passive continental margins at low latitudes where they typically form prograding or aggrading barriers (with growth during transgressive and highstand periods and erosion during longer low stand periods), or fringing reefs. By contrast, reef-forming toward the cratonward side of foreland basins is relatively rapid and reef geometries more aggradational. Finally, reefs forming in strike-slip basins and on thrust complexes are affected by the vagaries of local tectonic movements, which may be highly episodic but involve substantial displacements and are thus highly unpredictable (James and Wood, 2010).

Climate is a major controlling force on the evolution of reefs on both short and long timescales, as the latitudinal range of carbonate-producing species is largely governed by temperature and carbonate supersaturation. Reef growth therefore shows cyclicity at all scales in response to short-term oscillations (e.g., Milankovitch and glacial–interglacial cycles) as well as to longer-term climatic intervals, driven by slower, tectonically driven processes.

Global climate has oscillated through greenhouse and icehouse phases, in concert with aragonite and calcite seas, respectively. During icehouse times of continental glaciation, high eustatic sea-level changes created aggrading reef growth, common subaerial exposure and conspicuous regional disconformities in reef complexes. These large changes in sea level caused ramps to have steep gradients, and platform tops to have significant depositional relief characterized by pinnacle reefs and erosional topography. Icehouse reefs are typically dominated by heterotrophs or autotrophs with aragonitic or high-Mg mineralogies.

During greenhouse times, with little global ice, reef sequences were generated by small sea-level fluctuations. Reef cycles typically consist of very shallow-water facies, with regional-scale tidal flat caps and minor unconformities. Greenhouse reefs are often either compound or progradational as reef growth could easily match or outpace the fastest rates of sea-level rise. Ramps often have very low gradients, and platforms tend to be progradational, with minor topography. Greenhouse reefs can also have a more extensive range as carbonate settings extend into higher latitudes due to elevated global temperatures. Composition may also be more uniform, often dominated by low-Mg calcite skeletal components.

Biological disturbance, that is bioturbation, boring, and excavatory predation and herbivory, has clearly escalated since the Mesozoic. Reef biotas have responded with the proliferation of traits with proven anti-predatory benefits, particularly regeneration after partial mortality. Indeed some modern dominant reef taxa, such as branching corals and coralline algae, appear not only to thrive, but actually require conditions of considerable disturbance for their survival in shallow tropical seas (Wood, 1999, 2002).

Many modern reefs are largely reduced to rubble and sand via physical abrasion and bioerosion. Modern coral reefs are also dominated by branching forms due to their high diversity and abundance, propensity to proliferate via fragmentation, and resilience to taphonomic destruction. Many reefs prior to the Jurassic show the preservation of intact, in situ frameworks. Most epibenthic, soft-sediment dwelling organisms typical of Paleozoic reefs appear to have become largely absent from shallow marine tropical reef biotas during the late Paleozoic to early Mesozoic, perhaps due to intolerance of the rise of deep burrowing taxa and excavatory attack (Wood, 2010).

Scleractinian corals, in particular branching taxa, show a marked increase in the proportion of forms with complex modularity from the Eocene onward, even though corals displayed the full range of morphological forms and corallite size by the Late Triassic. Highly defended, thick crusts in coralline algae become more dominant, and branching forms also become noticeably less conspicuous on reefs from the Eocene onward. This major reorganization of the coral reef ecosystem coincides with the rapid appearance and radiation of herbivorous and coral-eating reef fish, but this remain to be tested experimentally (Wood, 2002).

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## GEOMORPHIC ZONATION

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## Introduction

The coral reefs of the Atlantic, the Caribbean and the Indo-Pacific do not differ fundamentally in their structural forms, their habitats and the interaction of their species, even though the organisms occupying specific ecological roles vary greatly between oceans and even between individual reefs. Goreau et al. (1979, p. 135)

Despite the similarity between the geomorphology of coral reefs noted by the Goreaus and others (Wells, 1957; Stoddart, 1969), much of the emphasis in characterizing coral-reef zonation has been ecological using either statistically defined coral assemblages or more simply,



the morphology of the corals themselves (Wells, 1957; Rosen, 1975; Geister, 1977; Pichon, 1978; Chappell, 1980; Done, 1982; Done, 1983). Most of these studies have found that shallow coral assemblages show a distinct zonation as wave energy, and hydrodynamic disturbance varies with depth and margin exposure. For example, Done (1982) found that shallow communities changed with a decreasing cross-shelf wave exposure in the central Great Barrier Reef. Individual reefs also showed the same pattern, with shallow-wave-adapted communities being replaced along leeward margins by upward shifts in the positions of deeper communities. Growth form of corals also show similar zonation patterns in response to depth and exposure-related variation in wave energy (Pichon, 1978; Chappell, 1980; Madin and Connely, 2006). Such zonation patterns have led to a clear distinction between rough-water reefs exposed to trade-wind-, swell-, and storm-generated wave fields and calm-water reefs protected from them (Geister, 1977, 1980).

A comparison of zonation schemes, however, shows that the coral assemblages in each zone can be highly variable on both inter-reefal and regional scale, and there is a significant overlap between the members of each assemblage zone (e.g., Done, 1982). Despite this “coral-scale” variability, the geomorphology of these reefs is very similar. Indeed, equally similar reef structures are produced in areas with order-of-magnitude differences in species abundances, and even where reefs have depauperate species numbers, their basic geomorphology is identical (e.g., Glynn et al., 1996). This consistency implies that gradients in wave exposure not only control the main environmental tolerances of shallow coral assemblages but also the form of the structures they build (Graus et al., 1977; Graus et al., 1984, 1985; Graus and Macintyre, 1989). It therefore follows that reefs might be better classified according to their geomorphic form (Wells, 1957).

Until very recently, a synoptic view of reef geomorphology showing the impact of varying ecological processes has not been possible, and previous attempts to summarize information have had to rely on parochial descriptions of what was accessible or visible at the time (e.g., Hopley, 1982; Guilcher, 1988). Following this approach, vast areas of modern reefs have been inadequately characterized and, with some exceptions, quantitative differences and the similarities between different regions have gone undocumented. This deficient situation is about to change. The recent advent of widely available orthorectified satellite imagery (Google Earth) and rapid development and cost reduction in geographic information systems, multi-beam sonar, LiDAR, and other remote-sensing technologies are making large-scale morphometric quantification of reefs feasible (Naseer and Hatcher, 2001; Andrefouet et al., 2001; Storlazzi et al., 2003; Naseer and Hatcher, 2004). As such, we are on the cusp of being able to provide a more holistic view of modern coral-reef form and a development that will provide

timely insight into the resilience and resistance of reefs to human-induced global environmental change.

In this entry, I examine satellite imagery using Google Earth along with local descriptions of reefs and attempt to summarize what is presently known about the geomorphic zonation of well-ordered, rough-water reefs, outline their formative processes, and assess their development.

### Standard geomorphic reef zonation

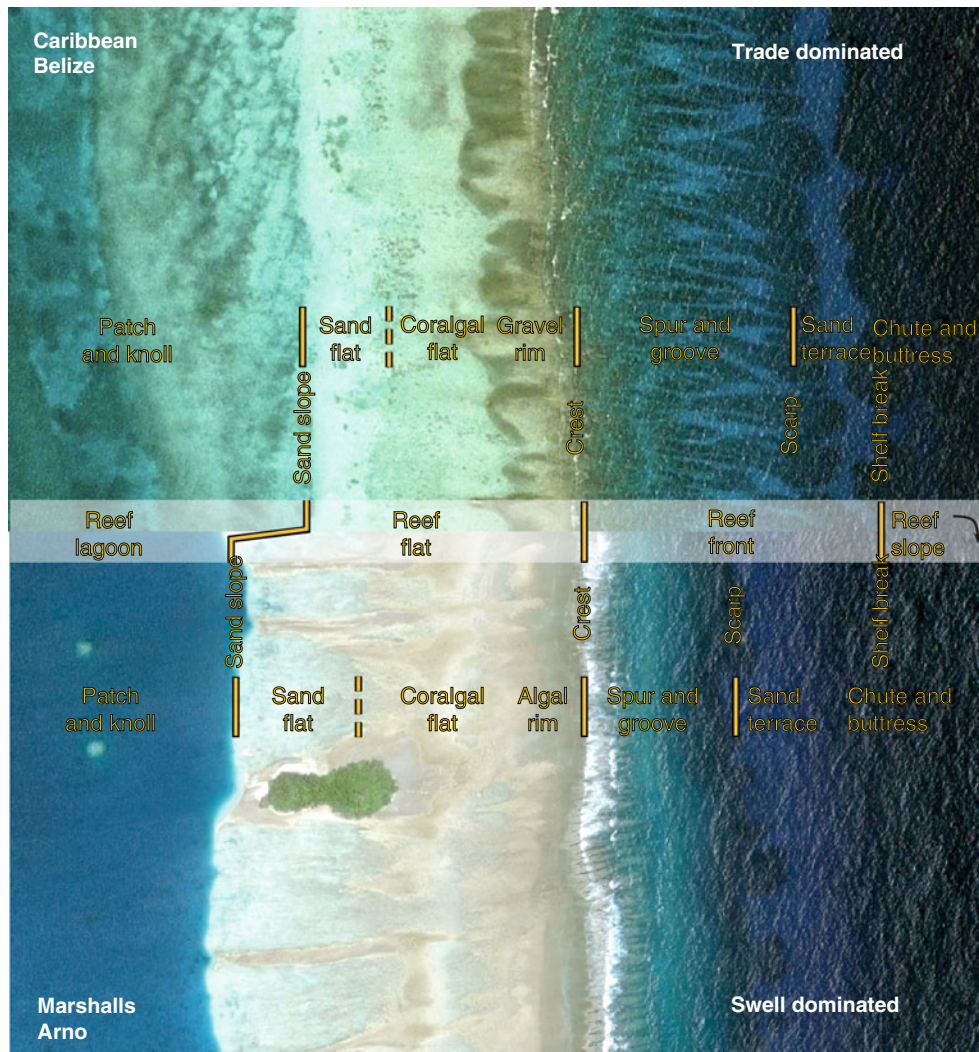
A comparison of well-ordered, rough-water reefs shows a remarkable degree of conformity between the size and character of their major morphological features (Figure 1). All of them consist of five first-order or “standard” zones: a calm reef lagoon, with varying number of patch reefs; a largely barren, shallow reef flat strewn with detritus; a narrow, gently sloping reef front exposed to waves and swells; a steeper reef slope bearing corals to as deep as 100 m; and a less steeply inclined fore-reef apron, where coral and reef detritus accumulate. The boundaries between these standard zones are delineated by simple slope breaks. The break between the lagoon and the reef flat is either a sand slope or a small reef scarp. The break between the level reef flat and the gently sloping reef front occurs at the reef crest. Similarly, the shelf break separates the gently sloping reef front from the steeper reef slope, and the break between the reef slope and fore reef is the transition into slopes that reflects the angle of sediment repose. Each of these standard and easily defined reef zones can in turn be subdivided into commonly recurring second-order zones or subzones, which may not be present on all reefs and, if they are present, may vary between margin, area, and region. As a consequence, their boundaries can be more difficult to define.

### Lagoon

With their calm, stable environments, and depth ranges that are usually within the range of coral growth, lagoons potentially represent an ideal and extensive habitat for reefs (Figure 2). The actual variation in lagoonal reef development however is striking, and even in areas where lagoonal reefs are prolific, such as the Tuamotus, there are examples where reefs are completely absent (Adjeroud et al., 2000; Paulay and Kerr, 2001).

### Patches, knolls, and pinnacles

Lagoons with significant reef development show two main types of subcircular structures, patch reefs and knolls. Patch reefs reach mean sea level and rise from substrates <20 m deep; where the substrate is deeper, they are termed pinnacles. Knolls are submerged reef patches but can also develop into pinnacles where they have >20 m relief (Stoddart, 1969). Patches, knolls, and pinnacles can develop in a dispersed pattern or can become connected to form linear ridges with various arrangements (e.g., Maxwell, 1968; Hopley, 1982). Dispersed patches or knolls have a density continuum from widely spaced to a point where they connect with



**Geomorphic Zonation, Figure 1** Geomorphic zonation of rough-water reefs. Both swell- and trade-wind-dominated reefs develop five standard reef zones: lagoon, reef flat, reef front, reef slope, and fore reef (not shown). These zones are delineated by simple slope breaks: the sand slope between lagoon and reef flat, the reef crest between the reef flat and reef front, the shelf break between the reef front and reef slope, and the break between the subvertical lower slope and the talus cones of the fore-reef sediment. These standard zones are divided into several widely occurring subzones, which vary with respect to margin orientation, area, and region. Images copyright of Google Earth, DigitalGlobe and GeoEye, 2010.

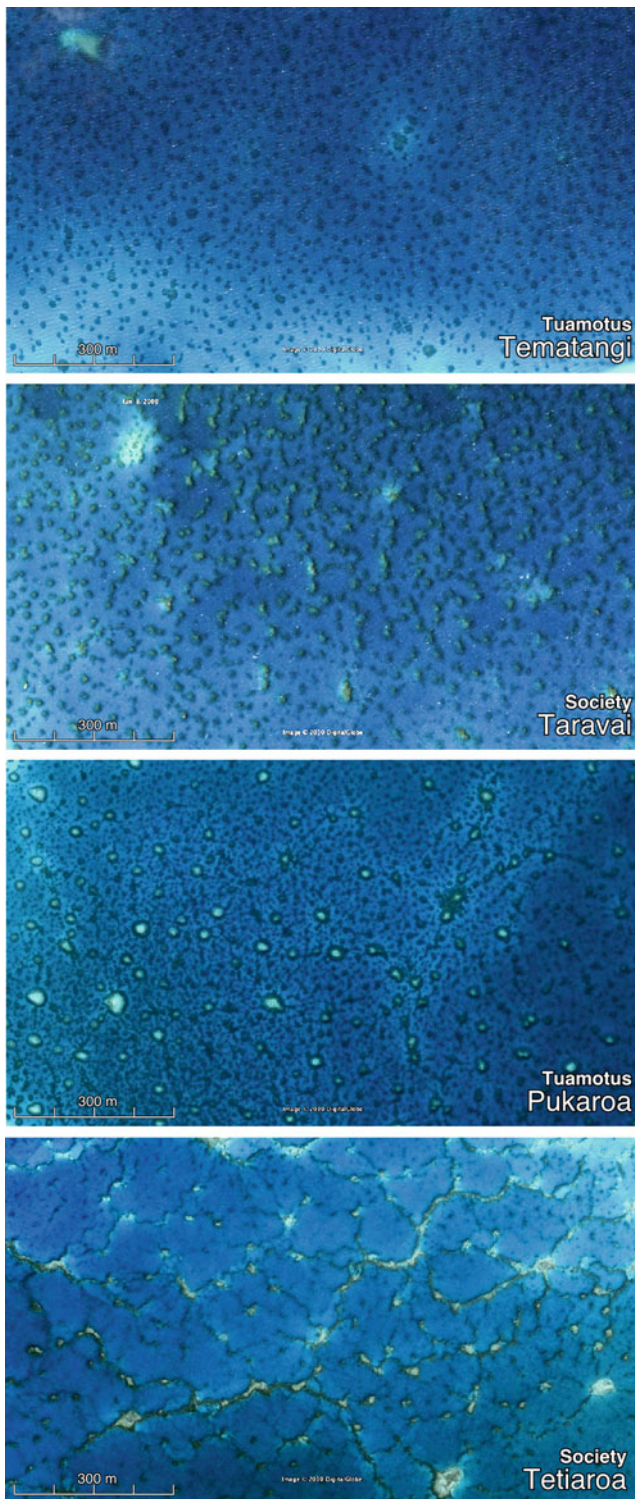
neighbors (Figure 2). Connected patches or knolls can further develop into ridges with sinuous, stellate, or reticulate arrangements, with the latter closing off distinct areas of deeper water, producing a cellular pattern of reef development. This cellular structure develops at various scales and can produce cells as large as 1,000 m in diameter (Figure 3).

Many lagoonal reefs have diverse coral assemblages, which can develop a distinctive windward/leeward as well as depth zonation (Wells, 1957). In Tikehau, for example, emergent patch reefs are topped by skeletal sand and cobble-sized coral gravel. The windward side has large head corals of 6 m, and leeward and deeper sides are covered by branching acroporids to depths of 15 m

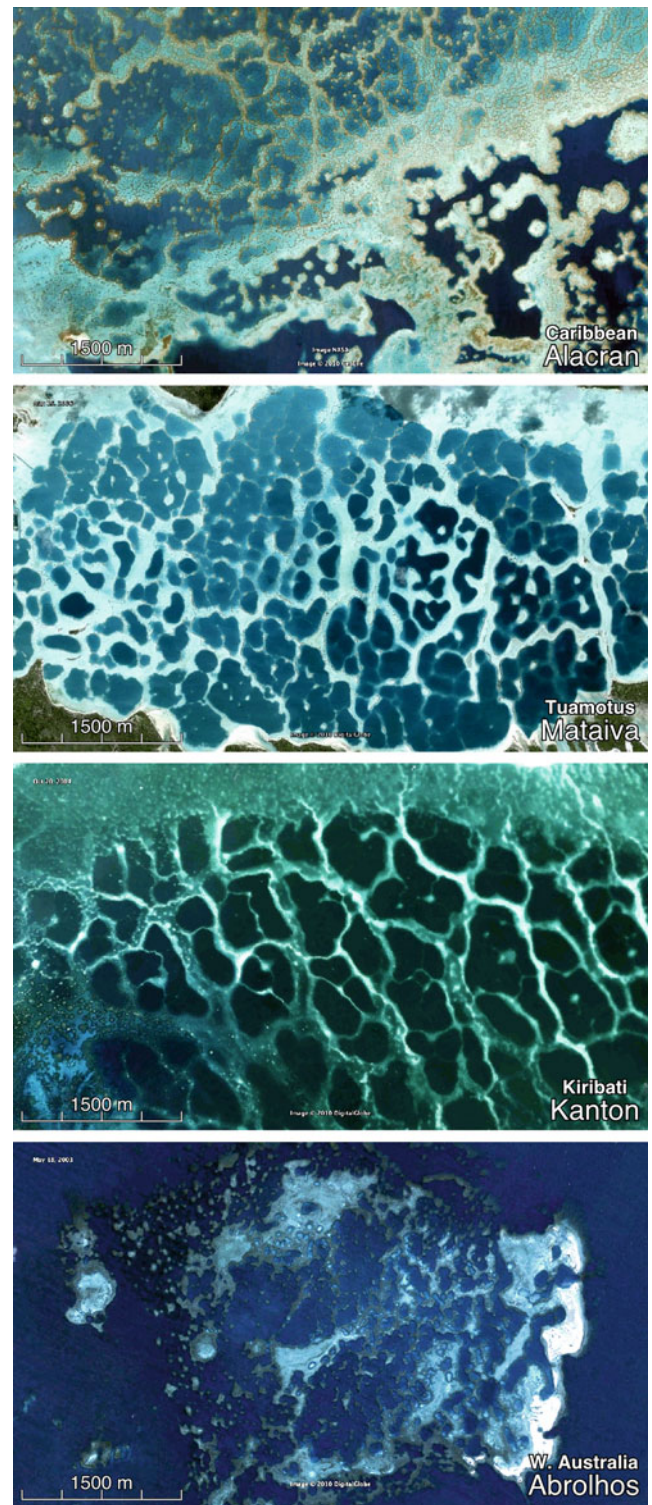
(Intes and Caillart, 1994). In addition, there can be lateral gradients in coral zonation within individual lagoons as a consequence of various environmental gradients (Paulay and Kerr, 2001).

An obvious control on lagoonal reef development is the degree of water exchange with the open ocean. During World War II, causeway construction blocked spillways over reef flats and isolated lagoonal sections, causing mass mortality of corals (Maragos, 1993). This led to the realization that a dominant exchange mechanism was related to reef flat currents driven by wave setup and not necessarily to tidal exchange (Atkinson et al., 1981; Andrews and Pickard, 1990). This has been most clearly demonstrated by Callaghan et al. (2006), who showed that during most





**Geomorphic Zonation, Figure 2** Lagoonal reef development showing the varying arrangements and densities of patch reefs (emergent) and knolls (submerged). Images copyright of Google Earth, DigitalGlobe and GeoEye, 2010.



**Geomorphic Zonation, Figure 3** Reticulate reef development in lagoons shown at the same scale to emphasize the varying scales of cells enclosed by reticulate networks. In the case of Houtman-Abrolhos, subsurface data show that the networks are the result of coral growth during the Holocene. Images copyright of Google Earth, DigitalGlobe and GeoEye, 2010.



of the tidal cycle, incident wave energy on the windward margin pumps water onto reef flat and into the lagoon, while water exits over the leeward reef flat and through channels. Wave pumping causes lagoon water levels to remain above the ocean at all tidal phases and to rise significantly during periods of enhanced wave activity (see also Kraines et al., 1999). As a consequence, exchange is directly related to the proportion of reef flat that is submerged or dissected by channels and, where tidal channels are narrow or absent, island formation and sediment deposition on the reef flat can play a key role (Kench and Mclean, 2004). The impact of water exchange and wave pumping on lagoonal reef development has been clearly illustrated in the Tuamotus, where Adjeroud et al. (2000) reported that reef pinnacles were more abundant and diverse in bigger atolls, which had either large channels or a high proportion of submerged reef flat. Conversely, they found that smaller atolls with reduced exchange due to reef-flat island formation were typified by low pinnacle abundance and diversity.

### Cellular reefs

Reef development in lagoons can also be self-limiting due to a negative feedback between growth and circulation. For example, prolific development of pinnacles in protected lagoonal areas of the Houtman Abrolhos reef complex, off the western Australian coast, has produced a cellular reef pattern, as shown in Figure 3 (Collins et al., 1996; Wyrwoll et al., 2006). The reef tops have a dense cover of branching acroporids, which only extend 7–10 m down the steep walls of the cells. In some areas, the walls overhang and show collapse scars, which expose open frameworks of the same corals; the floors of the cells are between 10- and 30-m deep and covered with a thick skeletal sand and branch-coral gravel. Their water columns are stagnant and stratified and do not support coral growth below 10 m. Drill cores and seismic data confirm that these cellular reefs are composed of branching acroporid frameworks that developed during the last 7–10 ka over a flat Pleistocene reef terrace at ~40-m depth (Collins et al., 1996; Wyrwoll et al., 2006). These studies in the Houtman-Abrolhos show that the prolific growth of branching acroporids has led to the coalescence of isolated pinnacles into reticulate structures that have enclosed deeper cells, causing restricted circulation and self-limitation of coral growth. Reticulate and cellular reef development is therefore one of the several examples of self-organization in coral reefs and is an emergent property of the synergy between rapid lagoonal reef growth and circulation.

### Formation of lagoonal reefs

The development of lagoonal reefs, particularly cellular reef forms, has been persistently linked to antecedent karst due to its similarity to polygonal and cockpit-cone forms that develop in humid tropical karst terrains (MacNeill, 1954; Purdy, 1974; Purkis, 2010). However, as alluded to above, drilling and seismic profiling has consistently

shown that reef forms are growth induced, either developing from scratch during the present interglacial or continuing atop development that took place during previous interglacial stages (Harvey and Hopley, 1981; Hopley, 1982; Smith et al., 1998). On Cocos-Keeling, seismic data collected by Searle (1994) showed that the modern reticulate reef development was largely growth induced but was influenced by a combination of fossil reef growth as well as karst-induced collapse structures in the underlying substrate. In other areas, positive relief provided by previous episodes of interglacial reef growth has likely played a negative role in modern lagoonal reef development. For instance, the rims of Pacific atolls are often multigenerational reef structures, which developed during previous interglacials (e.g., Szabo et al., 1985); where these rims are continuous, they must have prevented lagoonal reef development for significant time intervals until the sea level overtopped them and initiated their modern structure ~8 ka ago. This delay in development may explain the anomalous paucity of reefs in some of the deeper modern atoll lagoons.

For other forms of lagoonal reef development however, antecedent substrates have provided little to no guidance for subsequent events. On John Brewer Reef on the Great Barrier Reef (GBR), Walbran (1994) obtained seismic profiles showing that both lagoonal patch reefs and the reef rim are underlain by a flat Pleistocene surface at 20-m depth. The same was also found at Heron and Sykes reefs in the Capricorn Group by Smith et al. (1998) and in the Houtman-Abrolhos reef complex by Collins et al. (1996). Modern reef growth in lagoons and other zones is clearly capable of generating its own structures with little help from antecedent templates of any kind.

### Reef flat

In contrast to the high-relief patches and pinnacles of the lagoon, reef flats are remarkably level surfaces and their low-tide elevation varies little for hundreds of meters. If there is any gradient at all, it tends to slope back from the outer reef flat toward the inner, and its lagoonal margin water depths are no more than 1–3 m. In the absence of islands and storm ramparts, the width of open reef flats in atoll groups such as the Marshalls and Tuvalu is between 500 and 1,000 m, but exceeds this in the Tuamotus and Maldives where flats with widths of 2,000 m are common. The presence of islands and storm ramparts however tends to significantly reduce reef-flat width by impeding sediment transport into the lagoon. As recognized by Hopley (1982), open reef flats consist of two common subzones: an outer “living zone” composed of an algal rim and a coral algal flat and an inner sand zone mantled by thin sheets of shifting sediment (Figure 1).

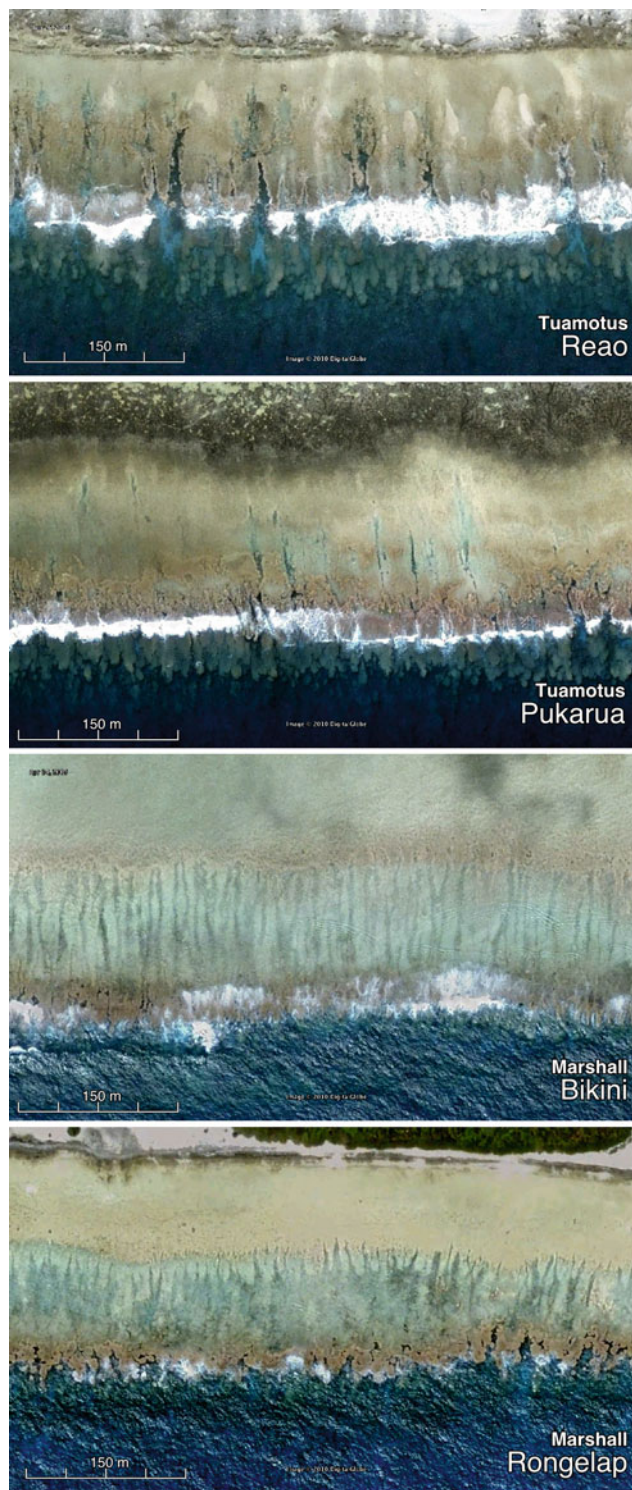
### Algal rims

Algal rims are usually less than 50-m wide and form the highest part of the reef flat. Two types of algal rim are

common and have been described from the Marshalls, Tuamotus, Tonga, and the southern Maldives (Tracy et al., 1948; Ladd et al., 1950; Wells, 1951; Newell, 1954; Wells, 1957; Stoddart, 1966; Nunn, 1993). The first type is an elevated  $\sim 1$ -m-high ridge (above mean low water) fronting the most exposed reef sections, normally associated with islands (ridges as high as 2.5 m have been reported from the southern Tuamotus where storm swell is severe; Salvat and Salvat, 1992). This high ridge type is commonly dissected by surge channels, 1-m wide and as much as 3-m deep, which are inshore extensions of reef-front grooves that have been narrowed by corallines (Figure 4). These channels extend back into the reef flat for 30–100 m and drain water pumped onto the flat under large swells or strong trade wind conditions. The channels can become completely roofed over and develop blow-holes surrounded by terraced coralline mounds that rise to as much as 1 m above the surrounding reef flat. The regular spacing of channels divides the algal ridge into buttresses, which form the heads of reef-front spurs (Tracey et al., 1948). The second type of algal rim develops on open reef flats and consists of a broader arch that rises less than 0.5 m but is not dissected by surge channels. Less commonly, rims consist of groups of pillars, piers, or buttresses that have been roofed over by corallines to form room-and-pillar structures (Tracey et al., 1948). Sheltered pockets and caverns in these complex structures can be capacious and may support limited coral communities. But in general, algal rim substrates are dominated by crustose corallines, particularly *Porolithon onkoides*, which requires continuous disturbance from wave surge to prevent competitive exclusion by fleshy algae (Littler and Doty, 1975). General rates of accretion of this coralline have been measured up to 10 mm/year (Steneck, 1986; Adey and Vassar, 1975), but these are clearly sufficient to build and maintain algal rims.

### Coralgal flat

A good proportion of the reef-flat zone is covered by a coralgal flat, which is an intertidal platform composed mostly of coral gravel, crustose corallines, and scattered corals. Coral cover tends to rapidly diminish away from the rim due to the increasing temperature and salinity variations in the shallow waters of the reef-flat interior (Wells, 1951). The highest coral cover is usually found in a broad trough developed immediately behind the low algal mound type along open flats (Wells, 1957). Here luxuriant patches of coral cover 50% of the surface and develop up to low tide. Between corals, the gravel substrate is stabilized by crustose corallines to form a smooth pavement. In front of islands, where there is less coral cover, the trough is clearly seen to be crossed by rimmed, partially roofed, or filled surge channels whose spacing reflects that of the reef-front grooves (Figure 4). Behind the trough is a largely barren surface covered only by a few centimeters of water at low tide. In places, several generations of eroded algal-ridge remnants protrude above the flat



**Geomorphic Zonation, Figure 4** Reef flats forming in front of islands, showing algal ridges, back-ridge troughs cut by surge channels, and the coralgal zone. Surge channels align with reef-front grooves and provide evidence of reef-flat progradation. In the Marshalls, this has occurred in jumps producing wide troughs. Images copyright of Google Earth, DigitalGlobe and GeoEye, 2010.



surface by as much as 1 m and clearly represent former positions of the algal rim (Ladd et al., 1950; Scoffin et al., 1985). Also protruding are boulders of coral framework eroded from the reef front and thrown up onto the reef flat during cyclones. These become welded to its surface by corallines and often develop an intertidal notch produced by intense bioerosion (Stoddart, 1969).

On other swell-dominated reefs, troughs are absent and the coralgal flat behind the rim consists of a very distinctive striated zone, especially in areas with high tidal ranges such as the GBR and western Indian Ocean. This consists of elongate strips of reef flat consolidated by corallines, sometimes colonized by corals, and separated by furrows of unconsolidated skeletal sand and gravel, which deepen and widen inshore (Hopley, 1982). Although coral cover varies, the furrows are persistent features, which can extend across the entire coralgal zone. At Mayotte, sand and gravel stripes clearly continue in alignment with the reef-front spur and groove, and have a height differential of 10–50 cm. At Mahé in the Seychelles, 2–3-m-high stabilized gravel ridges narrow inshore and are separated by 1–2-m-deep furrows, which widen and deepen inshore (Guilcher, 1988).

### Sand flat

The innermost sides of open reef flats, adjacent to the lagoon, are dominated by shifting sand that is either washed back from the seaward rim or, when winds switch direction during storms or monsoons, from the lagoon itself. The predominant movement of sediment in this zone occurs during tropical cyclones when large amounts of sand covering islands in the reef-front reservoir is remobilized and deposited as spill-over lobes, which prograde into the lagoon, forming a distinctive sand slope. This general sediment movement into the lagoon is interrupted by islands, which provide shelter from sedimentation and foster patch-reef development along this boundary. These patches can become well developed and form a linear reef with a steep lagoon-side scarp.

### Islands and storm deposits

Low-lying sand islands, and their associated channels (hoas) and gravel ramparts, constitute a large proportion of swell-dominated reef flats and form features which are dynamic in both space and time. Although these features are formed by a combination of storm and fairweather processes (Kench and Brander, 2006), storms assume a greater importance because they generate gravel through the destruction of corals, remobilize inactive sediment deposits on islands and in sub-wavebase reservoirs, and provide a continuous force on geological timescales. For these reasons, storms likely play a major role in initiating island formation and causing major subsequent changes (Baines et al., 1974; Bayliss-Smith, 1988). Reports of the impacts of tropical cyclones indicate that, in addition to erosion, three kinds of reef-flat deposit are common: outer-flat gravel bars, coastal ramparts along

existing islands, and aerially extensive gravel sheets over both the flat and islands (McKee, 1959; Blumenstock, 1961; Baines et al., 1974). The outer-flat gravel bars are composed of cobble to boulder-sized coral clasts, which are eroded from the reef front and typically deposited 20–30 m inshore from the algal rim. Under fairweather conditions, these gravel bars rapidly migrate inshore and are eventually left as marine cemented lenses of gravel spread out over the reef flat ~100 m from the outer rim; these are known as conglomerate platforms (Hopley, 1982). Such immobile lenses commonly provide a locus for subsequent sedimentation, and storms can add extensive shore-attached gravel ramparts for considerable distances along and between platforms (Baines et al., 1974). However, the most volumetrically important reef-flat deposits consist of thin but aerially extensive sheets of finer-grained cobble to pebble gravels that can become rapidly stabilized either in island settings by marine vadose cements to form “cay rock,” or on open reef flats themselves by crustose corallines (Newell and Bloom, 1970; Marshall and Jacobson, 1985). Successive deposition and cementation of gravel lenses and sheets can produce island platforms that reach 2 m or more above present mean sea level. Dating of these platforms in several areas has yielded anomalously old ages and, as a result, it has been claimed that they represent widespread reef-flat development during a regionally higher mid-Holocene sea level (e.g., Dickinson, 2004) despite the fact that clasts in these deposits have large age ranges (e.g., Scoffin et al., 1985).

### Formation of reef flats

The paucity of active coral growth and the flatness and low-tide elevation of many Indo-Pacific reef flats have been a continued source of confusion and, as alluded to, the age and origin of gravel deposits have provoked particular controversy (e.g., Newell and Bloom, 1970). A persistent idea is that reef flats have been eroded to their present low-tide level by a slight fall in regional sea level over the last several 1,000 years (e.g., Cloud, 1952). A variation of this has been advocated by Pirazzoli and Montaggioni (1988) and Woodroffe (2008), who suggested that the relative sea-level fall during past few millennia has produced many emergent reef flats, which are developed at elevations too high to be suitable for coral growth. This implies that reef flats were constructed by coral framework prior to the inferred sea-level fall; yet, drill cores through reef flats consistently show that they are not composed of thick framework but of detrital deposits (Henny et al., 1974; Marshall and Jacobson, 1985). Hence, the present reef-flat surface is a reflection of its interior, and an absence of corals and low-tide elevation does not require an erosional explanation. In addition, elevation data used to infer higher sea level have not accounted for elevated water levels on reef flats due to wave pumping and ponding of water behind storm ramparts, and elevations used from relict algal ridges are



commonly no higher than their modern counterparts. And even where they are, possible changes in wave climate in controlling their elevation rather than sea level are not taken into account. Moreover, in all of the reef-flat studies claiming regional sea-level highstands, the error range of the sea-level indicator is the same magnitude as the sea-level change itself (Woodroffe and Horton, 2005). Thus, claims that modern reef flats are somehow palimpsest and have been modified by falling sea level lack adequate support.

Other analyses of reef-flat form and zonation have assumed that flats did not develop until reefs caught up with sea level, despite the fact that the evidence for reef catch-up in most areas is equivocal due to inadequate core coverage (Blanchon and Blakeway, 2003). For example, Hopley (1982) proposed a retrogressive model of reef-flat development on the Great Barrier Reef in which presumed catch-up reefs progressively developed a zoned reef flat through time as reef framework and sediment migrated into the lagoon. A prediction of this hypothesis is that deposits should get younger toward the lagoon; yet, drill cores consistently show the opposite, with reef-flat ages increasing toward the lagoon in almost all the areas studied in sufficient detail (Easton and Olson, 1976; Pirazzoli et al., 1987; Randall and Siegrist, 1988; Takahashi et al., 1988; Kan et al., 1997a; Scoffin and Le Tissier, 1988; Woodroffe et al., 2000).

This widely documented pattern of inshore reef-flat ageing is more consistent with progradation, whereby the algal rim builds seaward out over the reef front through time (Ladd et al., 1950; Pirazzoli et al., 1987). Indeed, such a pattern would not only explain why reef flats are flat, with no space for framework accretion, but it would also account for many of their morphological features. For example, the widespread occurrence of back-rim troughs and surge channels extending 100 m or more into the reef flat interior is a key indication of this process (Figure 4). Imagery from the Marshall Islands in particular indicate that back-rim troughs represent shallow spur and groove that were abandoned due to algal-rim development along their leading edges (see Bikini and Rongelap, in Figure 4). The jump in the rim position to the spur front consequently left a shallow trough between the old and new rim that provided space for coral growth. In many areas, coral growth and gravel deposition rapidly filled this trough and only surge channels remain as evidence of its existence. In this way, reef flats can prograde rapidly and produce an extensive flat surface devoid of coral growth that is punctuated only by abandoned algal rims and boulder thrown up during storms. Why algal rims are periodically abandoned and jump seaward is related to the dynamics of spur-and-groove development, which is outlined below.

### Reef front

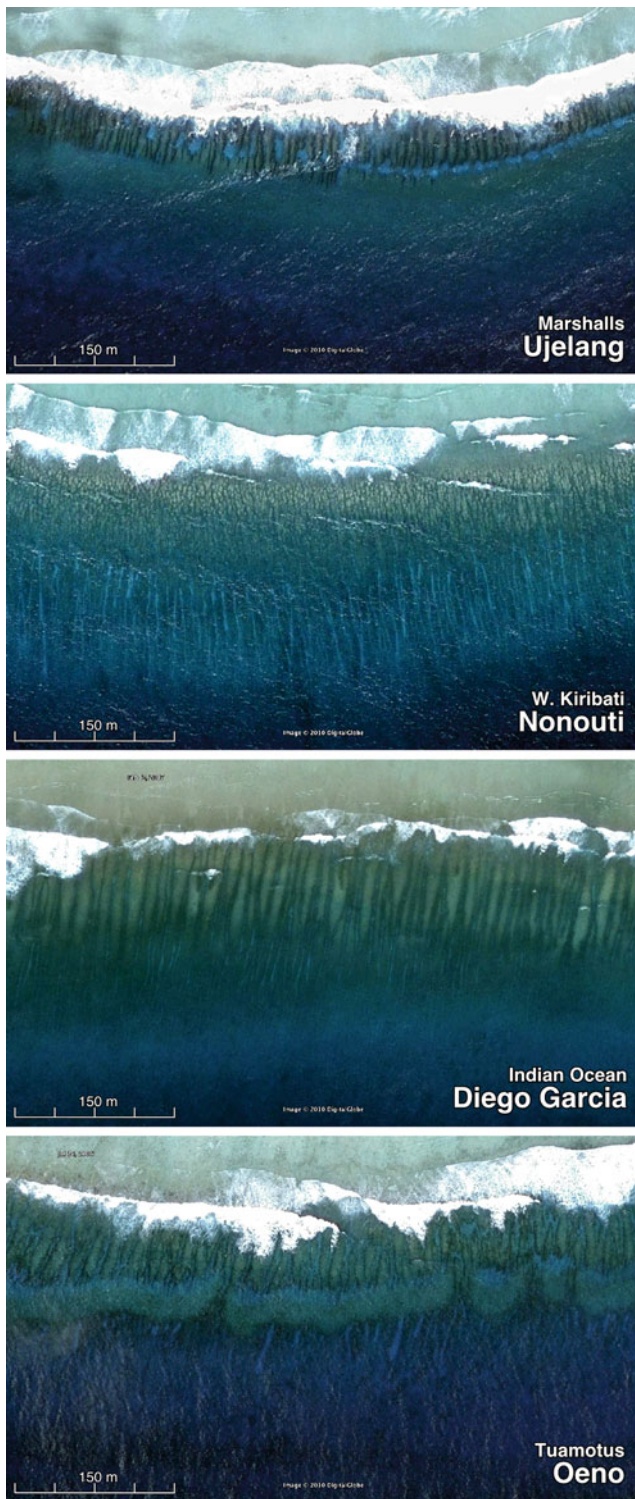
The reef front zone extends from the reef crest to the shelf break which, in many areas, occurs between depths of

20 and 50 m. This shallow zone is perhaps the most distinctive of all reef environments and consists of narrow annular subzones, which show remarkable concordance between regions. As shown in Figure 1, reef fronts on swell- and trade-dominated reefs generally consist of three common subzones: a shallow spur-and-groove zone, which extends down to a mid-shelf slope break around 10 m, followed by a relatively low-gradient sand terrace at 15–25 m, which passes into a chute and buttress zone developed over the shelf break and down the reef slope. In all of these subzones, reef development is molded by wave scour during both fairweather and storms and forms a characteristic cross-shelf sequence of elongate spur systems. In shallow water, scour is also responsible for sculpturing exposed bedrock surfaces into ridges and furrows, with ridges becoming enhanced by coral colonization (Allen, 1982; Blanchon and Jones, 1995). Unfortunately, due to the rigors of collecting data in such wave-swept areas, reef development in these subzones is poorly known and core data exists only for the greater Caribbean with no reports for any Indo-Pacific reef fronts.

### Spur and groove

Spur and groove is a general term for regularly spaced arrays of buttresses and channels, which extend across the shelf (Figure 5). Two types of shallow spur and groove are common: one dominated by coralline algae and the other by corals. These systems are not mutually exclusive however and their distribution and form is controlled by wave energy (Munk and Sargent, 1954; Roberts, 1974; Sheppard, 1982; Blanchon and Jones, 1997; Storlazzi et al., 2003). Both coral and algal spurs can be present along the same high-energy swell-dominated reef front: a shallow high-energy surf-zone system, dominated by crustose coralline algae (see Ujelang and Oeno, Figure 5), and a lower-energy coral-dominated system that either develops downslope in slightly deeper waters (see Nonouti and Diego-Garcia, in Figure 5) or in an equivalent position along the leeward margin (Sheppard, 1981; Glynn, 1996). Furthermore, the frequency of spurs shows a correlation with water depth (and hence wave energy): surf-zone systems have a spacing of one spur every 6–10 m, whereas in deeper-water systems, such as the chute and buttress zone (see below), spurs are spaced every 30 m or more, largely as a result of greater spur widths and wavelengths (Blanchon and Jones, 1997; Storlazzi et al., 2003). Surf-zone spur systems extend seaward from the reef crest for 50–100 m dependent upon the shelf slope, whereas deeper water spur systems can be more extensive, and submerged terraces can be covered by coral spurs for several kilometers.

In high-energy swell-affected reefs, shallow spur-and-groove systems are dominated by coralline algae and extend seaward from algal rims parallel to wave orthogonals (Munk and Sargent, 1954; Sargent and Austin, 1954). Spurs are commonly 4–8-m wide and have steep, sometimes overhanging, sides; intervening grooves are



**Geomorphic Zonation, Figure 5** Shallow reef-front spur and groove. In the cases of Nonouti and Diego-Garcia, algal spurs pass into coral-covered spurs further downslope, whereas in the cases of Ujelang and Oeno, algal spurs pass into a bedrock sculptured into ridges and furrows by storm-wave scour. Images copyright of Google Earth, DigitalGlobe and GeoEye, 2010.

1–3-m wide and 2–8-m deep and are commonly floored with coral gravel that is moved only during storms. At their seaward ends, spurs have an amplitude of 5–8 m and terminate in waters 5–10-m deep (Tracey et al., 1948; Ladd et al., 1950; Cloud, 1952; Newell, 1956; MacNeil, 1972; Pichon, 1978; Sheppard, 1981; Intes and Caillart, 1994; Glynn et al., 1996). Spurs narrow seaward and can be straight-sided with a smooth surface or more irregular and covered by protuberances (Figures 4 and 5). Near surf base, the surface of spurs are covered only by patches of slow-growing crustose corallines or fleshy algal turfs, whereas below it small corals with reptant growth forms are common between the corallines (e.g., Intes and Caillart, 1992; Glynn et al., 1996). In the Marshall Islands, Munk and Sargent (1954) found that the grooves showed a bimodal frequency distribution that corresponded to the northeast trades and, during the summer, to swell from the southeast trades of the southern hemisphere. Also their depth and length were proportional to the wave period, so that the wave up-rush traveled the length of the surge channel and impeded up-rush of the next wave on its return. This, together with friction along the sides of the channels, was sufficient to dissipate wave energy and make spur and groove an effective natural breakwater.

In lower energy trade-wind reefs protected from swells, spur systems also form parallel to wave orthogonals but are covered by corals and composed of coral framework and extend seaward from gravel-dominated rims (Shinn et al., 1981, 1982; Blanchon and Jones, 1997). The fundamental difference between algal- and coral-spur systems is simply that coral spurs lack a thick, extensive cover of corallines, and this allows storms to regularly prune their coral cover and supply the crest and flat with copious amounts of coral gravel (Blanchon and Jones, 1995, 1997). Coral-line algae only play a significant role in stabilizing and binding this gravel (e.g., Macintyre et al., 2001).

### Formation of spur and grooves

Although the development of algal spur systems is poorly known due to the absence of core data, limited excavations and drilling on the outer reef flat support a growth origin (Henny et al., 1974; Marshall and Jacobson, 1985; Szabo et al., 1985; Glynn et al., 1996; Kan et al., 1997b). At Clipperton Atoll in the eastern Pacific, for example, shallow excavations into the ends and sides of algal spurs revealed a 1-m-thick base of *Pocillopora* sp. framework overgrown by crustose corallines, which was overlain in places by similarly overgrown colonies of massive *Porites lobata* (Glynn et al., 1996). This same *Pocillopora*–*Porites* assemblage formed coral spurs directly downslope in front of the algal spurs, indicating a developmental progression from intermittent coral growth, storm disturbance, and coralline overgrowth through time. This process is supported by several observations. First, reptant colonies of *Pocillopora* are scattered over the deeper parts of the algal spurs between 3 and 7 m, which indicates that corals can grow on spurs up to the base of the surf zone

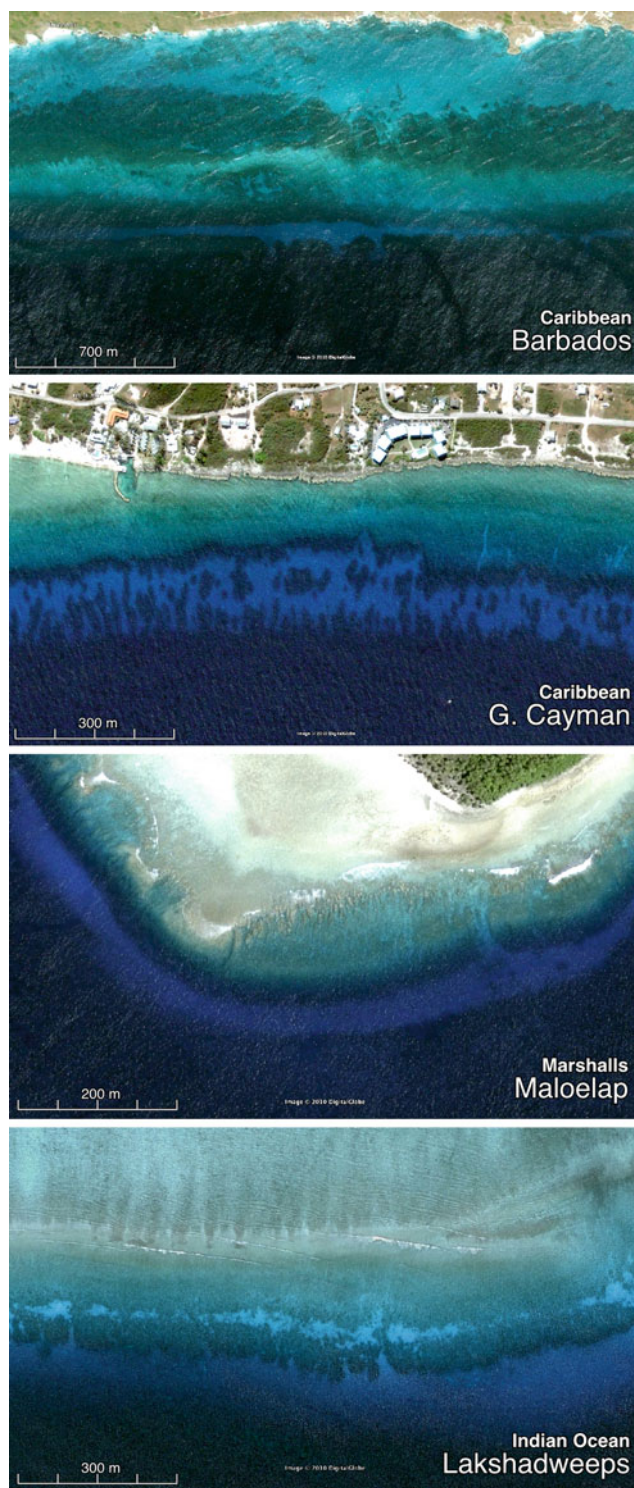


(Sheppard, 1982; Intes and Calliart, 1994). Second, coral growth in front of the algal spurs is largely dead and overgrown with crustose corallines (Glynn et al., 1996), indicating that the framework in these areas is rapidly stabilized and might be more resistant to removal or pruning during storms. These two observations imply that the distal spur ends have the highest potential for lateral and vertical accretion, which can proceed rapidly until they intersect with surf base at  $\sim 3$  m. From there, thick crusts of *Porolithon onkoides*, previously excluded due to fleshy algal overgrowth and surface grazing, causes a continued rapid accretion into the surf zone, leading to the upgrowth of a new algal ridge (Tracey et al., 1948). In this way, the process of distal spur upgrowth could not only facilitate spur development but also might drive reef-flat progradation over time. It also explains the problematic occurrence of double reef crests in several areas (Hopley, 1982; Guilcher, 1988).

More subsurface data is available for coral spur systems – mostly those from the greater Caribbean (Shinn 1963; Shinn et al., 1982a, b). In both Florida and Belize, for example, blasting and drilling indicate that shallow spur systems are composed of interlocking branched colonies of the surf-zone coral *Acropora palmata*, thickly encrusted by corallines (Shinn, 1963). Although this resembles the structure of algal spurs, the basal age of the coral spurs shows that they are older at their seaward end and get younger toward the reef crest, suggesting that they retrograded over their own back-reef deposits as sea level rose (Shinn et al., 1982a). Although the age structure of algal spurs is still unknown, ridge progradation indicates that spurs develop in the opposite direction and prograde seaward. If confirmed, this would be a major difference between these two types of spur system.

### Mid-shelf scarp and sand terrace

The area downslope from the shallow spur-and-groove system in water  $\sim 8$ –10-m deep, consists of a gently sloping bedrock terrace, which is either covered with coral spurs or is a bare rock ground, that has been sculptured by wave scour into low ridges and shallow furrows (e.g., Blanchon and Jones, 1995). This upper rock terrace is commonly terminated by a mid-shelf slope break before flattening out again into a lower sand-covered terrace, which extends out to the shelf edge (Figures 1 and 6). Both the slope break and sand terrace are frequently traversed by a system of widely spaced coral spurs between which thick deposits of skeletal sand and gravel accumulate. Being below the fairweather wave base, this sediment is only mobilized during storms, which ensures that the coral growth survives only on the elevated spurs. Coral gravel deposited at the end of the spurs is sheltered to some extent from wave scour, and subsequent colonization by corals during post-storm conditions ensures that spurs maintain their alignment with wave orthogonals and gradually extend out across the shelf. Where the sand terrace is



**Geomorphic Zonation, Figure 6** Reef-front mid-shelf scarp and sand terrace (or “10-fathom” terrace). Scarp best seen where reef growth is limited and commonly has an intertidal notch (as at Grand Cayman). Their presence around uplifting islands, such as Barbados, indicates an early Holocene sea-level origin. Images copyright of Google Earth, DigitalGlobe and GeoEye, 2010.



narrow, less sediment accumulates and more coral development is possible. Conversely, where the terrace is wide, a larger sand reservoir can prohibit spur development completely.

The sand terrace is a prominent feature seen in imagery from all oceans (Figure 6) and has been widely reported as the “ten fathom” terrace (Emery, 1961; Garrison and McMaster, 1966). Where it is not covered by excessive reef development, the terrace has been documented in roughly the same  $20 \pm 5$  m depth range from the following areas: the Marshall Islands (Tracy et al., 1948; Emery et al., 1954), the Caroline Islands (Tracey, 1968), the Tuamotus and Society Islands (Newell, 1956; Chevalier et al., 1968), Johnson Island in the central Pacific (Keating, 1985), Clipperton in the east Pacific (Glynn et al., 1996), the Solomon Islands (Stoddart, 1969), the Cocos-Keeling Islands and the Maldives in the Indian Ocean (Williams, 1994; Bianchi et al., 1997), the Bahamas and Caymans in the Caribbean (Blanchon and Jones, 1995; Newell, 1951), and Bermuda in the Atlantic (Stanley and Swift, 1968). In short, the slope break and the sand-covered 10-fathom terrace are ubiquitous geomorphological features and clearly represent the terrace and riser (cliff) of an abandoned submerged shoreline (Blanchon and Jones, 1995).

#### Formation of terrace-scarp reef-front features

Hopley (1982) argued that similar terraces on the Great Barrier Reef represented common levels of reef growth during glacial interstadials. A similar incremental explanation was suggested by Paulay and McEdward (1990), who simulated reef development over the last 125 ka. Both dismissed marine erosion as insignificant based on micro-erosion-meter measurements of fairweather coastal erosion (Spencer, 1985). However, mathematical modeling using more realistic erosion rates has demonstrated that marine planation is capable of producing terraces in all but the most resistant lithologies in less than 5 ka (Trenhaile, 1989). Furthermore, the presence of the sand terrace around islands with a history of uplift during the Pleistocene such as Barbados in the Caribbean and raised atolls in the Vanuatu chain, south Pacific, indicates that it must have developed during the postglacial rise in sea level (Blanchon and Jones, 1995). In fact, several drowned early Holocene breakwater reefs have been discovered associated with the terrace (Lighty et al., 1978; Blanchon et al., 2002). The crest of an 8-ka old reef was discovered around Grand Cayman along the inner edge of the terrace at a depth of  $\sim 20$  m, and its elevation corresponded with the position of an intertidal notch preserved in the mid-shelf scarp on the other side of the island (Blanchon et al., 2002). A correlation with similar elevations of drowned breakwater reefs, notches, and terraces developed around other islands in the Caribbean led Blanchon et al. (2002) to propose that these reefs and their shorelines were drowned by a meltwater pulse (Mwp-1c) during the early Holocene that was associated with the final

disintegration of the Laurentide Ice Sheet. The timing of this pulse is also consistent with further discoveries of drowned reefs in the Gulf of Carpentaria (Harris et al., 2008) and has been confirmed in several other non-reefal records of early Holocene sea level (e.g., Hijima and Cohen, 2010).

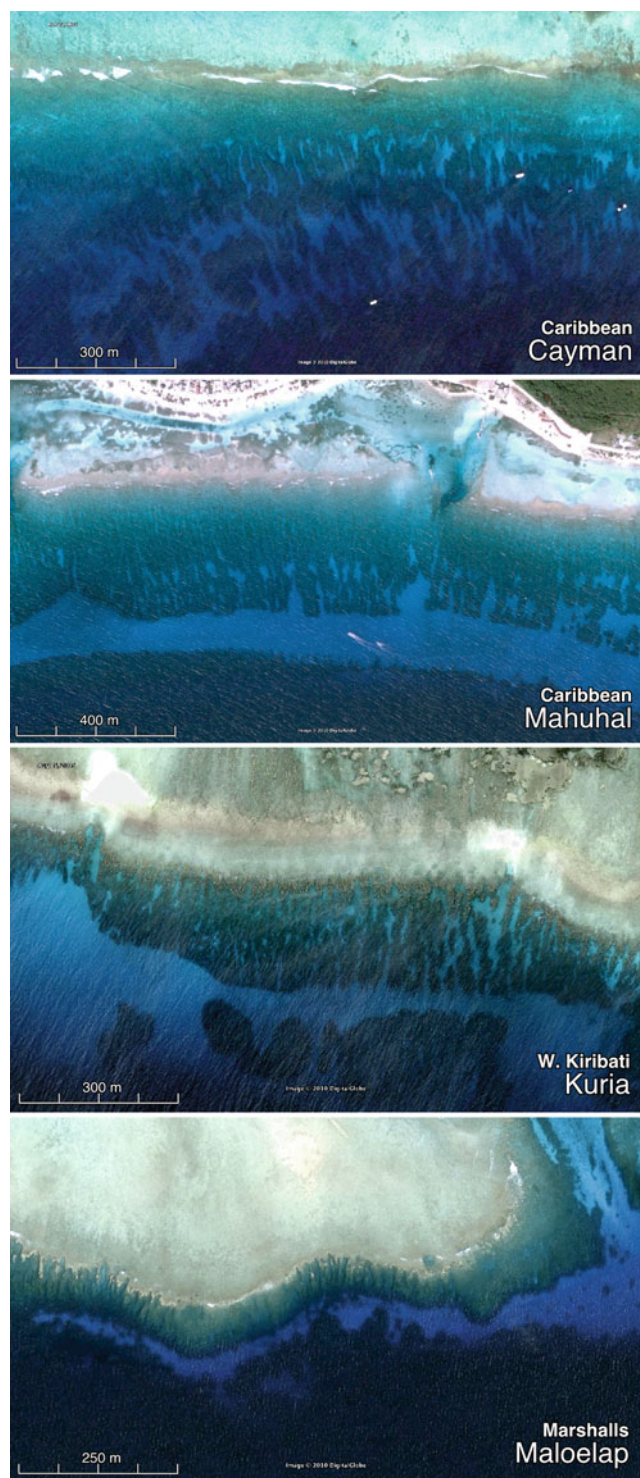
Much of the emphasis in these various explanations has been placed on the terrace-forming process. Yet, it is difficult to prove from these data alone if the terrace resulted from marine erosion or from incremental reef accretion. Also, it is no surprise that the terrace elevation differs slightly between reefs, given the variation in sediment and reef deposition during the Holocene; however, neither of these factors is particularly important to explain. This is because the notched scarp at the head of the terrace clearly shows it formed the shoreline behind reef crests that drowned during the 8-ka meltwater pulse. As a consequence, the presence of this scarp separating terraces in reef-front zones in other areas indicates that they too were subject to same shoreline development  $\sim 8$  ka ago. The surprising thing is that the notched scarp survived shoreface erosion during the subsequent sea-level rise and went on to influence reef development (Blanchon and Jones, 1995). Indeed, the preservation of notched scarps and abandoned reef crests in different oceans is testament to the sudden acceleration of sea level during that 8-ka meltwater pulse. It also explains why modern breakwater reef development in these areas did not start until after that 8-ka event (Blanchon et al., 2002).

#### Reef slope

In many areas, the reef slope is the most poorly known of the major geomorphic zones. It represents the outermost zone of reef construction and can be arbitrarily divided into two subzones: an upper subzone from the shelf break to the limit of effective coral-framework development at  $\sim 60$  m, and a lower subzone down to 120 m or more that may be dominated by a sciaphyllic framework of sclerospores, coralline algae, and microbialites. The geomorphology of this lower subzone has been modified by reef accretion but still bears a strong imprint of sea-level change during the last glacial–interglacial hemicycle (e.g., Anderson, 1998).

#### Shelf-edge chute and buttress (shelf-edge reefs)

Slope breaks associated with the mid-shelf scarp and shelf edge are often sites of preferential reef development because sediment bypasses these steeper areas on its way to depocenters on sand terrace and at the base of the reef slope, respectively; this is known as the “edge effect” (Porter, 1972). The shelf-edge site in particular is commonly associated with spectacular reef development (as shown in Figures 1 and 7), which has been described from various locations as either, sill reefs, shelf-edge reefs, or mesophotic reef systems (Goreau and Goreau, 1973; Burke, 1982; Blanchon and Jones, 1997; Lesser et al., 2009). This reef system develops from the brow of the



**Geomorphic Zonation, Figure 7** Submerged shelf-edge reef development. Accretion produces an array of buttresses with spurs that extend back over the sand terrace (see Grand Cayman) and down subvertical walls covered by platy corals to 60-m depth. Below that, platy coral cover is reduced and sclerosponges become more abundant. Images copyright of Google Earth, DigitalGlobe and GeoEye, 2010.

shelf edge at  $\sim 25$  m down the reef slope to  $\sim 60$  m and can extend laterally for tens of kilometers (e.g., Burke, 1982; Blanchon and Jones, 1997). These extensive shelf-edge reefs have generally been considered to be part of the main “reef complex” and have not been widely considered to be separate entities. However, several observations suggest otherwise: First, shelf-edge reefs commonly form along margins where breakwater reefs are absent (Blanchon and Jones, 1997). Second, they have been reported along the edge of much wider shelves where they are widely separated from breakwater reef complexes (e.g., Harris and Davies, 1989). In most areas however, these structures are juxtaposed along narrow shelves and, although influenced by similar processes, respond independently, producing distinctive reef architectures and biotopes (Figure 7).

One of the few characterizations of a shelf-edge reef system has come from the Caribbean Island of Grand Cayman (Blanchon and Jones, 1997). There, shelf-edge reef development extends around the full perimeter of the island (87 km) and forms an array of coral-covered buttresses separated by sediment floored chutes and canyons, which are aligned perpendicular to the shore (Figures 6 and 7). Individual buttresses consist of three elements: a subvertical front wall colonized by platy coral that plunges over the shelf edge; a dome-shaped crown covered by large head corals; and a shoreward-projecting spur covered by branching corals. On windward margins, these buttresses have an amplitude of about 10 m and their crowns rise to a depth of  $\sim 22$  m. In the most-exposed shelf sections, spurs have a frequency of one every 27 m and extend across the full width of the sand terrace to merge with the spur system covering the mid-shelf scarp. Along the less-exposed sections however, the spur length decreases and their frequency is reduced to one spur every 75 m. These trends also exist along more protected margins, and the spur frequency decreases in response to shelter from the ambient wave field. In addition, crowns rise into waters of 16 m and buttress amplitudes are reduced to  $\sim 7$  m (Blanchon and Jones, 1997). Along the leeward margin, buttresses merge to form an almost continuous sill reef dominated by branching corals and little spur development. This sill rises into waters as shallow as 12 m.

#### Formation of shelf-edge chutes and buttresses

Roberts (1974) found a correlation between shelf-edge buttress-spur orientation and vectorial properties of the wave field affecting Grand Cayman. From this, he conjectured that these deep-water spur systems had inherited the form of shallow spur-and-groove structures that were drowned as the sea level rose during the Holocene (Roberts et al., 1975). This was contested by Blanchon and Jones (1997), who showed that the lower frequency and more widespread distribution of shelf-edge spurs was inconsistent with this inheritance hypothesis. Instead, they suggested that the covariance between buttress area, amplitude, spur frequency, and local margin



orientation was more consistent with the varying destructive intensity of hurricane wave scour and approach angle (Blanchon and Jones, 1997; Blanchon, 1997). In other words, these shelf-edge reefs were produced by significant reef accretion in deeper waters. Although no drilling has yet proved this around Grand Cayman, cores from an extensive shelf-edge reef off Carrie Bow Cay, on the Belize Barrier reef, recovered an 11.6-m-thick section of domal and branching framework that developed over the last 5 ka (Macintyre et al., 1981). Similarly, 9 m of domal framework that had developed in the last 7 ka was encountered on a shelf-edge reef off the south coast of Barbados (Fairbanks, 1989). Off St. Croix, horizontal drilling into the front wall of a shelf-edge reef buttress by Hubbard et al. (1985) recovered 6 m of lateral accretion consisting of alternating detritus and domal framework. These thicknesses of framework are clearly sufficient to account for the amplitude of the shelf-edge reef buttresses and spurs in these areas and therefore support the contention that the shelf-edge reefs are independent structures controlled by ambient environmental processes (Macintyre et al., 1981; Blanchon and Jones, 1997).

### Lower reef slope

The upper section of the reef slope to ~60-m depth is dominated by a cover of platy corals associated with shelf-edge reef development; however, in the lower section of the slope below 60 m, this coral coverage declines rapidly, and by 100 m, generally forms a cover of less than 1%. In areas investigated by submersibles, this lower slope usually consists of a near-vertical wall with an irregular surface consisting of discontinuous, sediment-draped ledges and blind caves dissected by vertical chutes and gullies (Ginsburg et al., 1991; Grammer and Ginsburg, 1992). This irregular substrate is colonized by a sciaphyllid assemblage of sclerospoges, crustose coralline algae, microbialites, and platy corals, and their zonation and distribution are controlled by the light gradient, falling sediment from the shelf above, and the margin orientation (Goreau and Land, 1974; Land and Moore, 1977; Sheppard, 1982; Colin et al., 1986; Liddell and Ohlhorst, 1988; Ginsburg et al., 1991; Lesser et al., 2009). By far, the most thoroughly investigated lower reef slope is that along the north coast of Jamaica (Hartman and Goreau, 1970; Goreau and Land, 1974; Lang et al., 1975; Land and Moore, 1977; Liddell and Ohlhorst, 1988). In this area, the depth zone between 60 and 100 m consists of a variable cover of sclerospoges, with reports ranging from 7% to 25% and as much as 50% on the walls and ceilings of caves. In fact, in a cluster of caves between 80 and 90 m, Lang et al. (1975) reported sclerospoges as large as 1 m in diameter. Furthermore, a half-meter-deep blast site at 105 m exposed the sclerosponge framework with interstitial skeletal sediment cemented by high-magnesian calcite (Land and Moore, 1977). Similar abundances of sclerospoges have also been reported

from the Bahamas, where Ginsburg et al. (1991) estimated a cover of 5–25% in the same depth range.

### Formation of the reef slope

There is generally a very little subsurface data available concerning the development of reef-slope environments. The tendency of modern reefal margins to form steep precipitous slopes must relate to both accretion and erosion during rapid sea-level changes during glacial–interglacial cycles. For example, Blanchon and Jones (1997) suggested that the pattern of vertical and lateral accretion in shelf-edge reefs may explain the steep precipitous upper slope development that is common in many reefal margins. However, the vertical walls of the deeper lower slope must be related to the long phases of sea-level lowstands at 125 m or more that are associated with glacial stages (Land and Moore, 1977). Although these cliffs are presently covered by coral and sclerosponge frameworks and are likely undergoing some small amount of lateral accretion (e.g., Ginsburg et al., 1991), cliff recession rates during the extended duration of glacial lowstands must have been substantial. Therefore, the basic geomorphology of these vertical substrates is likely erosional – a claim that is supported by widespread reports of giant blocks of wall rock on forereef depositional slopes.

### Summary and conclusions

Rough-water coral reefs that develop in trade-wind-, swell-, and storm-dominated seas consist of five standard geomorphic zones: a back-reef lagoon, a reef flat, a reef front, a reef slope, and a fore-reef talus apron. These zones are separated by simple slope breaks: back-reef lagoons terminate at the sandslope break, reef flats terminate at the reef-crest break, reef fronts terminate at the shelf-edge break, and reef slopes terminate at the fore-reef talus break.

In lagoons, reef development can be extensive and reefs develop as dispersed knolls or patches that commonly merge to form ridges; these in turn can connect with other ridges to form complex reticulate networks that impede water circulation and self-limit their own development. In many lagoons, water circulation is a function of wind stress and exchange with the open ocean, with the latter process being controlled by a wave-pumping mechanism over open reef flats. Atolls with large sections of open reef flats therefore have better lagoonal reef development than smaller atolls, where the exchange system is more vulnerable to blockage by island formation in space and time. Seismic data show that the lagoonal reef form and development is not, as often claimed, inherited from a karstic substrate but entirely growth induced either from simple vertical and lateral accretion during the Holocene or from compound growth over previous interglacials.

Reef flats by contrast are remarkably flat intertidal platforms that can be several kilometers wide. They consist of an algal rim, an outer coralline flat, an inner sand flat, and a variable cover of low-lying detrital islands. The algal



rim, generated by the surf-adapted coralline *Porolithon onkoides*, forms the highest part of the reef flat and consists of either an elevated ridge fronting islands along the most exposed reef sections or a lower mound along more open flats. Behind the rim is an intertidal coralgal platform, veneered by a rapidly decreasing cover of corals and an increasing proportion of coral gravel stabilized by coralline algae. In its outer part, this platform can be punctuated by one or multiple remnants of former algal ridges whose age increases inshore or by large blocks of reef framework thrown up from the reef front during storms. In addition, the coralgal flat is commonly dissected by surge channels, which extend back into the reef flat in-line with reef-front grooves. Some flats are crossed by corals organized into narrow, parallel ridges that are separated by gravel-filled furrows, which also align with reef-front grooves. These various types of coralgal flats either grade into an inner flat dominated by shifting sands or pass directly into cobble rampart-fronted islands composed of a mix of storm-lain sand and gravels that can reach 4 m or more above the surrounding flat. Although stabilized by marine and meteoric cements, these gravel islands yield clasts with a large spread of ages, suggesting that they are commonly reworked by storms.

In explanations of reef-flat development, it has been argued that elevated islands, remnant algal ridges, and the extremely flat, barren nature of reef flats are a combined result of a late Holocene regional fall in sea level, which led to erosional planation of the surface to its present level. Several authors, however, have noted that these same features are consistent with processes that are presently active with a stable sea level. In fact, many of the key features of reef flats, such as their monotonous flatness, aligned features, and remnant ridges, can be accounted for by the simple seaward progradation of the algal rim out over the reef-front spur-and-groove zone through time.

Spur-and-groove development in shallow, rough-water reefs consists of two types: one with spurs covered by crustose coralline algae and the other with spurs covered by corals. On swell-dominated reefs, algal spurs extend seaward from the algal rim parallel to wave orthogonals and form high-frequency, steep-sided spur arrays, whose length is proportional to wave energy and the gradient of the seaward shelf. Coral spurs have a similar form and frequency but develop in lower wave-energy regimes either downslope from algal spurs or in an equivalent position along the leeward margin. All subsurface evidence collected so far point to a growth origin for both spur types, with algal spurs nucleating on downslope coral growth causing a seaward progradation through time, and coral spurs developing downslope from the crest and retrograding upslope through time.

The platform downslope of the shallow spur-and-groove terminates at about -10 m in a mid-shelf slope break that commonly takes the form of a small notched scarp (where it has not been covered by coral spurs or sedimentation). This scarp forms the riser to a distinct

sand-covered terrace, known as the 10-fathom terrace, which slopes from 20 to 30 m out to the shelf edge. This 10-fathom terrace and its scarp has been reported from all oceans and even around uplifting islands such as Barbados, and has become a depocenter for sediment accumulation and reef development during the Holocene. Discoveries of several early-Holocene breakwater reefs on the terrace prove that the notched scarp and terrace couplet represents a cliffed shoreline that formed around the same time and was drowned by a meter-scale sea-level jump ~8 ka ago.

The shelf break at the terrace edge is commonly a site of extensive submerged reef development, which has produced an array of sand chutes and steep-sided buttresses that form parallel to wave orthogonals. The buttresses, which can rise to 15 m and have amplitudes of 10 m or more, extend back over the terrace as a series of tapering spurs. To seaward, the subvertical face of the buttresses extends down the reef slope to ~60 m and has a dense cover of platy corals. Covariance between buttress area, amplitude, spur frequency, and local margin orientation indicates that the architecture of these shelf-edge reefs is controlled by hurricane wave scour and approach angle. Other suggestions that they developed over drowned breakwater reefs are not supported by drilling, which shows that shelf-edge reefs have produced greater than 12 m of vertical growth and 6 m of lateral accretion in the last 5 ka.

The reef slope beneath shelf edge reefs is commonly vertical below 60 m and is covered by an assemblage of sciaphyllic sclerosponges, crustose corallines, and microbialites. Although this assemblage is actively producing framework, the morphology of the deep reef slope has been significantly influenced by cliff collapse and mass wasting during the long intervals of glacial lowstands of sea level.

The remarkable similarity of reef geomorphology and architecture between and within oceans is a clear testament to their capacity for self-organization (Hatcher, 1997; Dizon and Yap, 2006). In other words, many of the features of these large-scale structures have emerged spontaneously from ecological processes operating at smaller scales. For example, the negative feedback between the simple vertical and lateral reef accretion and water circulation has produced extensive networks of cellular reefs in many lagoonal systems. Likewise, the simple interaction between wave scour and the colonization and growth of corals and crustose coralline algae has produced well-ordered spur systems with similar spacings at both local (windward-leeward), regional (trade or swell) and inter-oceanic scales. Finally, the interaction between herbivory and coralline accretion along the seaward edge of algal spurs may be responsible for intermittent seaward advances of reef flats through time.

Perversely, many of those responsible for interpreting large-scale reef development still cling to the paradigm that modern reefs are somewhat of a geological oddity and that their form and architecture are merely

a reflection of the underlying antecedent substrate – a position that would surely have Darwin turning in his grave. Although examples do exist of this substrate control, scaling-up of the concept to entire reef systems denies abundant evidence that reefs have built impressively thick, well-structured edifices during the last 14 ka, which have maintained their breakwater position as post-glacial sea level rose 120 m or more from its glacial low-stand. An understanding of the interactions and feedbacks that control reef organization during this development is key to assessing resilience and resistance of modern reef systems in the face of human-induced global environmental change.

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## Cross-references

Algal Rims  
 Blowholes  
 Boulder Zone/Ramparts  
 Double and Triple Reef Fronts  
 El Niño, La Niña, and ENSO  
 Fore Reef/Reef Front  
 Hydrodynamics of Coral Reef Systems  
 Lagoons  
 Megablocks  
 Moats  
 Patch Reefs: Lidar Morphometric Analysis  
 Platforms (Cemented)  
 Reef Flats  
 Reticulated Reefs  
 Spurs and Grooves  
 Submerged Reefs  
 Wave Set-Up

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## GLACIAL CONTROL HYPOTHESIS

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### Synonyms

Glacial control theory

### Definition

Hypothesis developed by R. A. Daly to argue for youthful, postglacial development of atolls and barrier reefs on platforms beveled during low sea surface temperatures and sea levels of glacial periods.

### ‘Glacial control’ of coral reef development

#### Development of the hypothesis

The glacial control hypothesis, developed and defended through a series of lectures, scientific papers, and book chapters between 1910 and 1948 by R. A. Daly, was an exploration of the effects of Pleistocene climate and sea-level change on coral reef evolution and morphology. The hypothesis should be seen in the context of Nathaniel

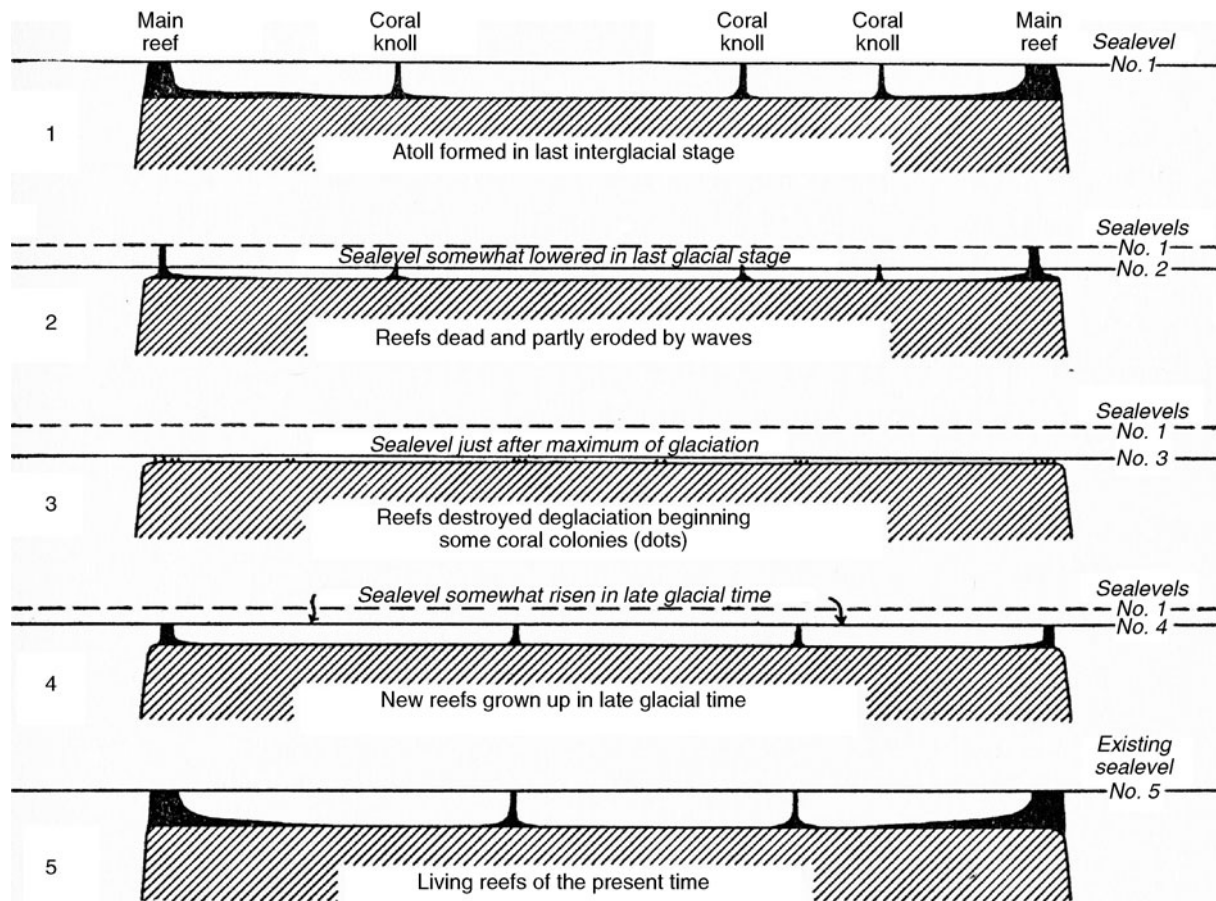
Shaler’s (1875) argument that sea level rather than the land was subject to general movement and Eduard Suess’s development of the idea of eustatic sea-level change in the second volume (1888) of “Das Antlitz der Erde” (translated by H. B. C. Sollas and W. J. Sollas as the “Face of the Earth” in 1906). Both Suess and Murray (1879–1880) favored the idea of the wave erosion of the summits of young volcanoes as providing a suitable platform for subsequent coral growth (and see also Steers and Stoddart, 1977 for ideas on planation surfaces and reef growth by Semper, Wharton, Guppy, and Gardiner).

Daly visited Hawaii in 1909 and observed the narrowness of the encircling reefs which he inferred as an indicator of young age; he saw evidence for recent glaciation on the volcanic slopes of Mauna Kea, indicating lower glacial temperatures; and he noted the closeness of contemporary sea surface temperatures in the northern winter at Hawaii to the threshold temperature for reef growth. These observations were built into the glacial control hypothesis, first published in 1910 and reaching their full development in the Silliman lectures delivered at Yale University and published in 1934 in a book entitled “The Changing World of the Ice Age.” W. M. Davis saw Daly’s hypothesis as diametrically opposed to Darwinian subsidence theory and submitted it to sustained intellectual attack (e.g., Davis, 1918, 1919, 1923, 1928) but, as Stoddart (1973) has pointed out, Darwin was concerned with understanding large-scale reef structure, whereas Daly was more concerned with explaining reef surface morphology.

Daly’s key fact, backed up by an analysis of bathymetric charts of reef areas, was the global accordance and planar nature of atoll lagoon floors and continental shelves in the reef seas within a limited depth range of 55–90 m. He argued that during the glacial periods, sea level fell, sea surface temperatures declined, and water turbidity increased. These processes, perhaps exacerbated by increased storminess and wave attack, resulted in coral mortality, the removal of dead coral framework, and the erosion of volcanic shores no longer protected by healthy reef structures. The outcome was the production of beveled platforms on volcanic islands and older limestone basements. As sea level rose and sea surface temperatures increased with the onset of interglacial conditions, then coral growth resumed, preferentially on the platform margins (where environmental conditions were most favorable for coral growth) to result in typical atoll and barrier reef morphologies (Figure 1).

### Tests of the hypothesis

The hypothesis encompasses several elements all of which are amenable to test as a result of late twentieth/early twenty-first century developments in Quaternary science. First, what was the degree of sea-level fall during the glacial periods? Second, what was the degree of sea temperature cooling during the glacial periods? And third, how easy is it to bevel a reef structure and produce a smooth platform?



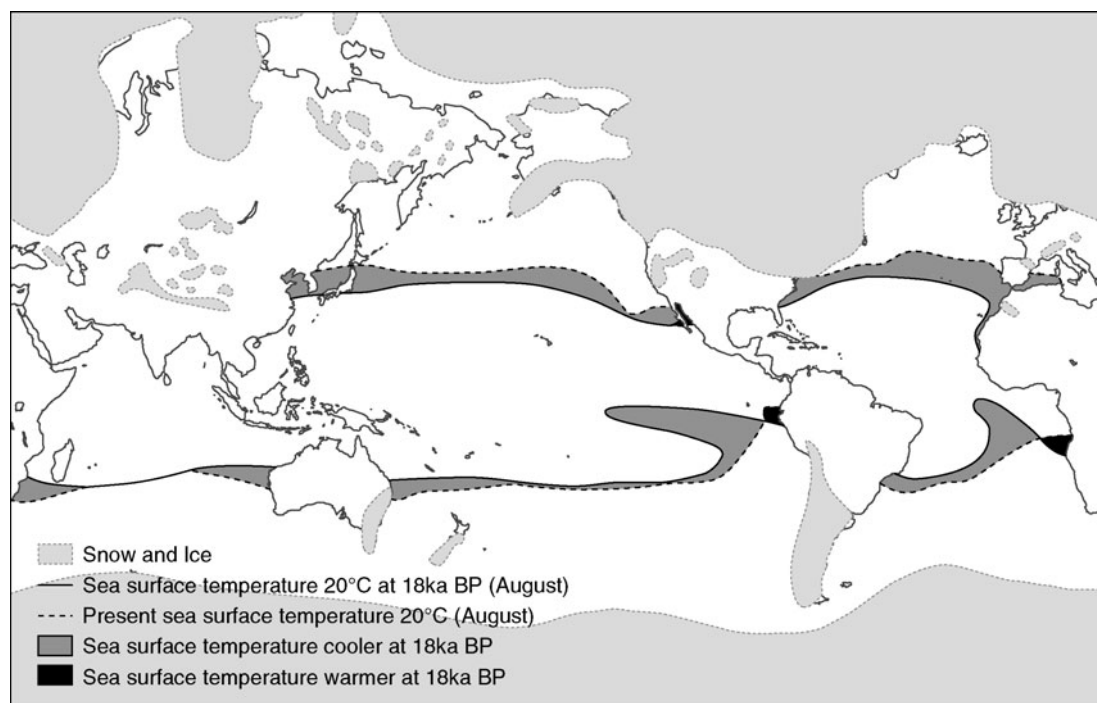
**Glacial Control Hypothesis, Figure 1** Sections illustrating aspects of the glacial control hypothesis of coral reefs. *Diagonal shading* indicates stable basement. 1: eustatic rise of sea level during the last interglacial stage giving new coral growth (in black), largely at the platform margin; 2: sea-level fall and water temperature decrease during the onset of the last glacial period, during which corals die and reefs are eroded; 3: at the Last Glacial Maximum reefs are destroyed and the bank is eroded to below the lower sea level; 4: the postglacial rise in sea level, together with a temperature increase, allows renewed coral growth (in black), particularly at the outer reef margins; 5: the present features of an atoll encircling a flat-floored lagoon. Source: Daly (1934).

Daly (1910) originally postulated a sea-level fall of 46 m at the glacial maximum which he then revised to a figure of 60–70 m, having dismissed the estimates of sea-level fall of 150 m as “excessive” (Daly, 1934, p. 165). It is now clear from drilling submerged *Acropora palmata* reefs offshore from the south coast of Barbados that sea level at the last glacial maximum (18 ka BP) was  $121 \pm 5$  m (Fairbanks, 1989).

For glacial sea surface temperature, Daly suggested a typical cooling of  $5^\circ\text{C}$ , with a maximum potential fall of  $10^\circ\text{C}$ . Quantitative reconstructions of last glacial maximum sea surface temperature, based on the microfossil and geochemical analyses of deep-sea cores, were first developed by the Climate Long-Range Investigation, Mapping, and Prediction (CLIMAP) project in the 1970s and 1980s (CLIMAP project members, 1976) and have recently been updated by the Multiproxy Approach for the Reconstruction of the Glacial Ocean Surface (MARGO) project. MARGO project members (2009) report an average mean

annual cooling at the last glacial maximum of  $1.7 \pm 1^\circ\text{C}$  for the tropical ocean between  $15^\circ\text{N}$  and  $15^\circ\text{S}$ . This can be disaggregated regionally into a cooling of  $2.9 \pm 1.3^\circ\text{C}$  in the Atlantic Ocean,  $1.4 \pm 0.7^\circ\text{C}$  in the Indian Ocean, and  $1.2 \pm 1.1^\circ\text{C}$  in the Pacific Ocean. There were, however, considerable temperature variations in the latter region: cooling of  $1\text{--}3^\circ\text{C}$  in the western Pacific Ocean warm pool, cooling of  $5\text{--}6^\circ\text{C}$  in the equatorial eastern boundary current along the Chilean coast but warming of  $1\text{--}2^\circ\text{C}$  in the subtropical gyres in both hemispheres. Daly claimed that “over wide stretches of the tropical seas the reef corals were exterminated or greatly weakened in their reef-building power” (Daly, 1934, p. 159). However, if the known falls in temperature are subtracted from the present patterns of ocean temperature isotherms for the coldest month, and the isotherm of  $20^\circ\text{C}$  is taken as the limit to effective reef growth, then the change in the area available for reef growth during the glacial periods can be illustrated (Slaymaker et al., 2009; Figure 2). This analysis shows that while Daly’s





**Glacial Control Hypothesis, Figure 2** Changing tropical ocean temperatures, Last Glacial Maximum to present, and implications for coral reef growth (from Slaymaker et al., 2009).

speculations on the magnitude of temperature fall were of the correct order of magnitude, his interpretation of their likely impact was incorrect. It was only on the very margins of the reef seas and in the area of the eastern boundary currents that sea temperature cooling was sufficient to cause a likely cessation of reef growth. Interestingly, these marginal belts were the one area where W. M. Davis was prepared to accept the occurrence of coral platforms of low-level abrasion, these being the only locations in the reef seas where cliffed volcanic island slopes can be seen on the margins of barrier reef lagoons (Davis, 1915, 1928).

Daly estimated that 50–200,000 years was available for platform abrasion and leveling in the periods of low sea level during the glaciations. This inference is broadly correct; environmental reconstructions from ice-cores and marine sediments in deep-sea cores show that lower than present sea levels have typically characterized 88,000 years of the characteristic 100,000-year long glacial–interglacial cycles of the last 500,000 years (e.g., Imbrie et al., 1993; Petit et al., 1999). While accepting that young volcanic islands were composed of erosionally resistant lava flows, Daly believed that most volcanic and coral islands were “composed of generally weak material” (Daly, 1934, p. 177) and that erosion rates of coral limestones would be comparable to the  $0.3\text{--}1.0\text{ m a}^{-1}$  retreat rates of the chalk cliffs in coastal southern England and northern France and that pyroclastic deposits and shelf sediments might be removed at rates comparable to the retreat rates of ca.  $2\text{ m a}^{-1}$  of the glacial cliffs on the UK Yorkshire coast of

the North Sea. Thus, there appeared to be no difficulty in beveling even large volcanic islands and extensive reef deposits in the time available, particularly if material had been weakened by previous phases of weathering and erosion under earlier glaciations. Recent quantitative measurements using the microerosion meter technique on shore platforms, over a range of materials and in different process environments around the world suggest, however, that erosion rates are several orders of magnitude lower than the rates used by Daly, with a mean rate of surface lowering of  $1.5\text{ mm a}^{-1}$  (Stephenson and Finlayson, 2009). Within this dataset, the erosional behavior of presently raised reef limestones provides an apt modern day analog for the reaction of reefs exposed by glacial falls in sea level. Such surfaces have been comprehensively investigated in two locations: at meso- to macrotidal Aldabra Atoll, western Indian Ocean by S. T. Trudgill (Trudgill, 1976a, b, 1983; Viles and Trudgill 1984) and at microtidal Grand Cayman Island, West Indies by T. Spencer (1985a–c). At Aldabra, mean intertidal rates of surface lowering were  $1.79\text{ mm a}^{-1}$ , varying between  $1\text{ mm a}^{-1}$  on low energy coasts to  $4\text{--}7\text{ mm a}^{-1}$  on exposed coasts. In the supratidal zone, the mean rate of subaerial erosion was  $0.26\text{ mm a}^{-1}$ . On Grand Cayman, the mean intertidal erosion rate was  $1.23\text{ mm a}^{-1}$ , varying between  $0.45$  and  $2.43\text{ mm a}^{-1}$  on reef-protected and exposed coasts, respectively (with bioprotection reducing rates to  $0.22\text{ mm a}^{-1}$  on the most exposed surf platforms). Subaerial downwearing was between  $0.45$  and  $0.97\text{ mm a}^{-1}$ . If these rates were characteristic of

the Pleistocene, then intertidal erosion would require 0.5–1.0 million years to plane a reef 1 km in width, well in excess of the time available in each glacial–interglacial cycle. Furthermore, shoreline retreat is an episodic rather than a continuous process in consolidated reef limestones, proceeding by alternating phases of intertidal notch cutting and then collapse. Next, intertidal backwearing is only part of the process of limestone removal, the other main process being solutional lowering of the exposed surface. On inland limestone substrates on Grand Cayman, mean subaerial erosion has been measured at  $0.37 \text{ mm a}^{-1}$ , with subsoil and submangrove rates of  $0.16 \text{ mm a}^{-1}$  and  $0.21 \text{ mm a}^{-1}$ , respectively. Thus if reefs were emergent by 125 m at the glacial maximum, then it would take over 300,000 years to remove such a column of limestone at the highest of these mean rates of lowering. Finally, the heterogeneity of lithification in reef limestones is reflected in the fact that erosion is extremely localized and gives rise to a pitted and cavernous microtopography rather than undifferentiated planation; thus, erosion is often accompanied by the preservation of original depositional reefal surfaces.

### Alternative explanations for the morphology of modern reef surfaces

It is clear from modern process studies that once reefs are formed they are difficult to remove by marine and subaerial erosion processes. In addition, the refining of the magnitudes and duration of ocean temperature change and sea-level fall following the late twentieth-century advances in environmental reconstruction do not provide the contexts within which wholesale reef removal can be realistically achieved. Given that present sea levels have been at or near to their present levels for at most the last 6,000 years and in some cases for only the last 1,000 years (only 0.6–0.1% of the last glacial–interglacial cycle), these conclusions suggest that the topography of modern reefs is often inherited from underlying, older reef surfaces (see also Chapter *Antecedent Platforms*). On the basis of bathymetric charts, Daly argued for the smoothness of these reef basements. Davis (1928) argued that such smoothness was the product of effective lagoon infilling during the upgrowth of marginal reefs. However, more recent detailed lagoon and shelf floor mapping, both of bottom morphology and, using seismic techniques, of bedrock surfaces below reefal sediments, has shown many basements to be characterized by highly irregular bedrock surfaces (Bloom, 1974), often organized into characteristic limestone erosional, or karstic, forms. Topographic features range in scale from small solutional features (e.g., solutional pipes in the Florida Keys; Dodd and Siemers, 1971) to marginal raised rims around saucer-shaped reef platforms (MacNeil, 1954; Harvey, 1977), “knoll and basin” topography in atoll lagoons (e.g., Chuuk lagoon, Federated States of Micronesia; Shepard, 1970), and “blue holes” in back-reef environments (e.g., Lighthouse Reef blue hole, Belize Barrier Reef; Stoddart, 1962), to large scale regional karst landscapes. The most comprehensive exposition of karstic control on

reef landscapes was provided by E. G. Purdy who, on the basis of seismic profiling and shallow drilling, argued that the regional morphology of the Belize Barrier Reef reflects a drowned doline karst in the drier northern barrier reef and on the central and southern barrier reef and a drowned tower karst in the lagoon and a flooded basement cockpit karst on the barrier reef margin itself. These latter two morphologies have resulted from the submergence of a karst marginal plain, supplied by solutionally aggressive drainage waters from the noncarbonate Maya Mountains. The underlying karstic control is clear on the Belize Barrier Reef because of the interaction of the depth below present sea level of the basement and the sea-level history at this location; Holocene reef development has been dominated by vertical, “catch-up” behavior and thus postglacial reef growth has exacerbated the underlying pre-Holocene topography (Purdy, 1974).

Elsewhere, the relations between basement depth, sea-level history, and postglacial reef growth modes (give-up vs. catch-up vs. keep-up) have been more complicated and given rise to a wider range of contemporary reef forms; in cases where the basement has been close to present sea level, reef growth may have completely filled the accommodation space and thus obscured any antecedent topography (Hopley, 1982). In some locations, the underlying antecedent topography is not a karst erosion surface but a depositional one and thus reef topography reflects colonization of stabilized carbonate shoal or reef top storm deposits (e.g., Garrett and Scoffin, 1977) or reef growth on underlying river levee (Choi and Ginsburg, 1982) or deltaic deposits (e.g., Maxwell, 1970).

### Conclusions

R. A. Daly’s “Glacial Control Hypothesis,” developed in the first quarter of the twentieth century, importantly engaged coral reef science with the question as to how reefs had reacted to Pleistocene changes of ocean temperature and sea level. Developments in Quaternary Science and in process geomorphology have, however, not supported Daly’s assumptions about the rapidity at which volcanic materials and coral reef limestones can be removed by erosion and thus the ease with which reefal surfaces can be planed to smooth lagoon floors and reefal shelves during the glacial phases of the Pleistocene. Rather modern reef topographies often reflect the complex underlying topography of much older, pre-Holocene surfaces and the erosional and depositional process histories to which they have been subjected. Antecedent topographic control is, however, variable and relates to the degree to which subsequent reef growth has either accentuated or obliterated the basement surfaces from which modern reefs have developed.

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## Cross-references

Antecedent Platforms  
 Belize Barrier and Atoll Reefs  
 Blue Hole  
 Climate Change and Coral Reefs  
 Daly, Reginald Aldworth (1871–1957)  
 Darwin, Charles (1809–1882)  
 Davis, William Morris (1850–1934)  
 Last Glacial Lowstand and Shelf Exposure



MacNeil, F. Stearns  
 Postglacial Transgression  
 Sea Level Change and Its Effect on Reef Growth  
 Solution Unconformities  
 Subsidence Hypothesis of Reef Development  
 Thickness of Holocene Reefs

## GLACIO-HYDRO ISOSTASY

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### Synonyms

Eustatic sea level; Glacial rebound; Postglacial sea level

### Definition

Glacio-hydro isostasy refers to the earth's response to changes in surface ice and water loading during glacial cycles. During the growth of an ice sheet, the crust is loaded in the areas of glaciation and the crust beneath and near the ice sheet subsides. During the decay phase of an ice sheet, the crust is unloaded and rebounds. This is the glacio-isostasy component. But as water is extracted from, or added into, the oceans during ice growth and decay, the oceanic crust also responds to the changing water load. This response is called the hydro isostasy. The two combined components, not uncoupled, are referred to as glacio-hydro isostasy.

### Introduction

The glacio-hydro isostatic effect is manifested in geological, geophysical, and geodetic observations. It is seen in the geological record as a complex spatial and temporal pattern of raised shorelines (Figure 1) in areas of former glaciation (primarily the glacio-isostatic signal) as well as along coastlines far from the former ice margins (primarily the hydro-isostatic signal). It is also seen in geodetic observations: as displacements of the crust, both vertical and horizontal; as sea-level change in tide gauge and satellite altimeter data; as changes in gravity measured by surface instrumentation and by satellite sensors and orbital perturbations; and as anomalies in the earth's rotation. It has implications for understanding sea-level change, paleogeographic reconstructions of coastal environments, archaeology, the stress state of the crust, and the computation of precise satellite orbits.

### Models for glacio-hydro isostasy

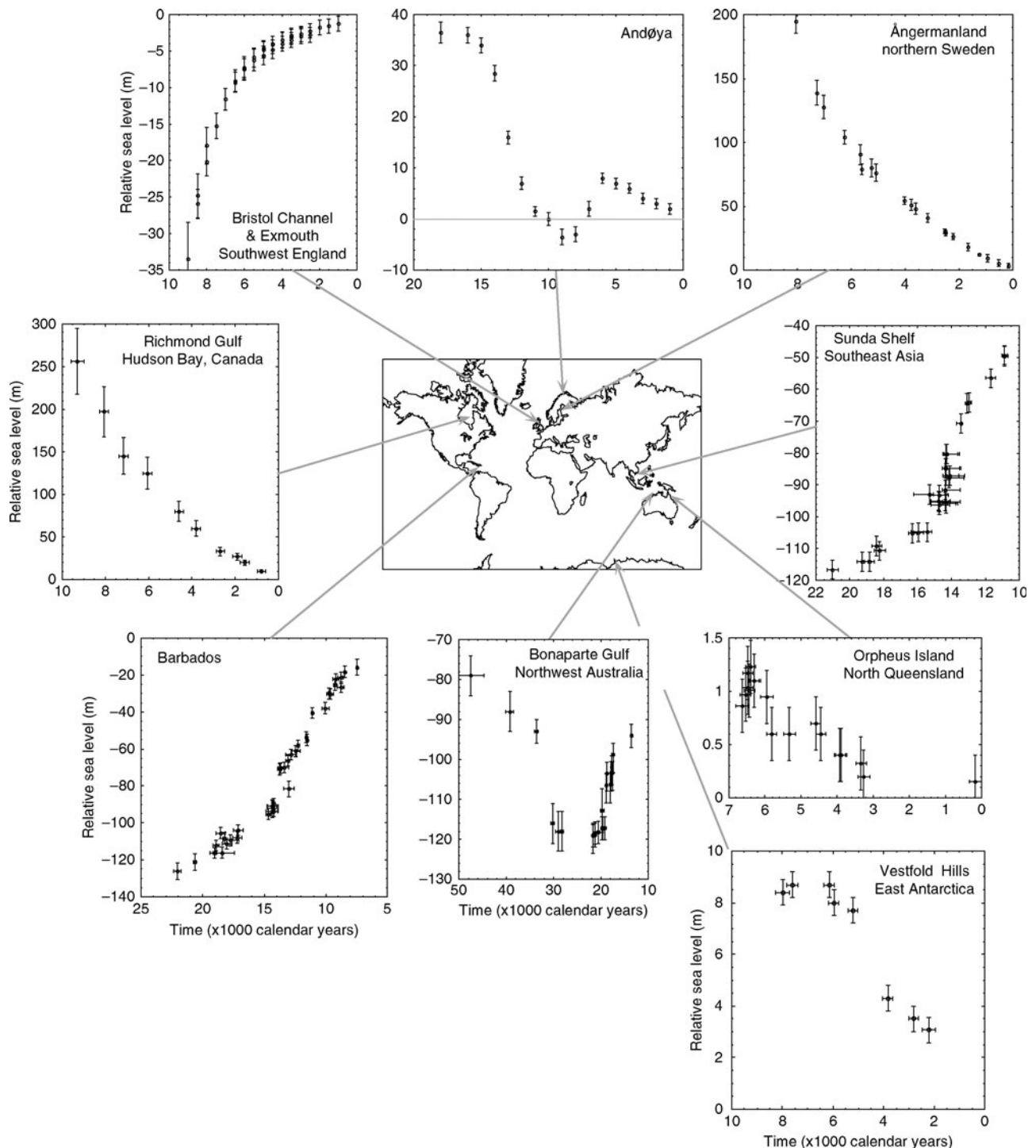
A zero-order description for isostatic response to loading is a model of local response of a crust–lithosphere that is unable to support shear stresses and that overlies a fluid mantle of zero viscosity. An ice load of  $H$  m thick and of density  $\rho_i$  would displace the crust beneath it by

$-H\rho_i/\rho_{\text{mantle}}$  or  $\sim 25\text{--}30\%$  of the thickness of the ice or water load. This model ignores the strength of the essentially elastic crust–lithosphere as well as the viscosity of the mantle, but it provides a useful order of magnitude estimate of the maximum displacement that may occur. Thus, beneath large ice sheets, the maximum crustal displacement may approach a kilometer and the seafloor within ocean basins may be displaced by 30–40 m for a globally averaged sea-level change of  $\sim 120$  m.

An improved model is one of regional isostasy in which the load is supported by an elastic crust–lithosphere layer that overlies a zero viscosity mantle. For loads of horizontal dimensions much greater than the lithospheric thickness, the displacement at the center is nearly equal to that predicted by the local model but at the edge of the load it is only about one half of this amount because the load is partly supported by the flexural strength of the lithosphere. Thus, along continental margins, the hydro-isostatic signal may reach 15–20 m for the above global sea-level change of  $\sim 120$  m. But this is still only an order of magnitude estimate and to fully describe the global pattern of sea-level change, more physically realistic models, that involve the mantle viscosity, are required.

Realistic models of the glacio-hydro-isostatic phenomenon include the following features:

- Physically realistic representation of the planet's response function, or rheology, to surface loading on timescales of thousands of years. The observational evidence indicates that the earth is still responding today to the unloading of the last great ice sheets such that the model requires elastic as well as viscous elements in the response function. For both mathematical expediency and because it provides a satisfactory explanation of the observational evidence, a linear viscoelastic response is usually assumed. Both depth and lateral variability in the rheology needs to be considered.
- A realistic description of the evolution of the ice sheets during the full glacial cycle. A detailed description of the individual ice sheets is required (on a  $0.5^\circ$  grid and preferably smaller) for the evaluation of the glacio-isostatic component, but for the hydro-isostatic component it is the total rate at which water is added or removed from the oceans that is the significant requirement.
- A detailed description of the ocean basin to ensure that meltwater from the ice sheets is properly distributed. This distribution has to satisfy the requirement that the ocean surface is an equipotential surface at all times and that the ice–water mass is conserved. Through time, the ocean basin deforms, the shorelines migrate and the ice sheets displace water on the shelves. The ocean basin deforms in response to both the ice and water loads and this introduces a coupling between the glacio- and hydro-components of the isostatic response.
- The ability to compute the deformation and the mass distribution of the earth–ocean–ice system through time and to relate this to the observational evidence for



**Glacio-Hydro Isostasy, Figure 1** Representative sea-level curves for different localities around the world. The time and sea-level scales are not the same for all examples. (After Lambeck and Chappell [2001]).

- sea-level change and shoreline migration, crustal deformation and gravity change, and the global inertia tensor.
- The feedback that occurs through the earth's rotation. As the inertia tensor is modified during the glacial cycle, the earth's rotation, centrifugal force, and the gravitational equipotential surfaces are also modified.
- High spatial resolution solutions are required. Sea-level changes above the threshold of observational

accuracies can occur, for example, over distances of 10 km or less across former ice margins or continental margins and the numerical solutions must be able to represent this.

The formulation of the glacio-hydro-isostatic rebound is well established but the definition of the rheological parameters or aspects of the ice models themselves are often less well known and are mostly inferred from the analysis of the rebound evidence. Thus, for descriptive purposes, the formulation serves as an interpolation device between fragmentary observational evidence that also allows for a degree of extrapolation beyond the limits of the time–space dimensions defined by the observational data.

### The sea-level response

In the context of coral reefs, the most important consequence of the glacio-hydro-isostatic response is sea-level change. Schematically, the equation describing sea-level change,  $\Delta\zeta_{\text{rsl}}(\varphi, t)$ , can be written as

$$\Delta\zeta_{\text{rsl}}(\varphi, t) = \Delta\zeta_{\text{esl}}(t) + \Delta\zeta_{\text{I}}(\varphi, t) + \Delta\zeta_{\text{T}}(\varphi, t) + \Delta\zeta_{\text{O}}(\varphi, t)$$

with

$$\Delta\zeta_{\text{I}}(\varphi, t) = \Delta\zeta_{\text{I-g}}(\varphi, t) + \Delta\zeta_{\text{I-h}}(\varphi, t)$$

$\Delta\zeta_{\text{rsl}}(\varphi, t)$  represents the change at location  $\varphi$  of the sea surface relative to land at time  $t$  compared to its present position at time  $t_{\text{p}}$ . The first term on the right-hand side represents the ice-volume equivalent sea-level contribution (ESL) and is a measure of the globally averaged sea-level change due to a change in ice volume. It is defined as

$$\Delta\zeta_{\text{esl}}(t) = -\frac{\rho_{\text{i}}}{\rho_{\text{o}}} \int_t \frac{1}{A_{\text{o}}(t)} \frac{dV_{\text{i}}}{dt} dt$$

$V_{\text{i}}$  is the ice volume at time  $t$  and includes the ice mass on continents and grounded on continental shelves.  $A_{\text{o}}(t)$  is the ocean surface area and is defined by the shoreline and the grounding lines of any ice on the shelves, both at time  $t$ .  $\rho_{\text{i}}$ ,  $\rho_{\text{o}}$  are the average densities of ice and ocean water. In the absence of any other factors that lead to changes in ocean volume, the ice-volume equivalent sea level is equal to eustatic sea level.

The second term,  $\Delta\zeta_{\text{I}}(\varphi, t)$ , is the combined isostatic contribution. It is schematically divided here into two contributions: the glacio-isostatic part  $\Delta\zeta_{\text{I-g}}(\varphi, t)$ , and the hydro-isostatic part  $\Delta\zeta_{\text{I-h}}(\varphi, t)$ . Both terms include contributions from the deformation of the crust under the time-dependent surface load and from the change in the gravitational potential of the earth–ice–water system (sometimes referred to as geoid changes). Coupling between the two isostatic terms arises from the deformation of the ocean basins and from the change in gravitational attraction by the ice. This is ignored in this

schematic description but not in the actual models (Lambeck et al., 2003; Mitrovica and Milne, 2003).

The third term,  $\Delta\zeta_{\text{T}}(\varphi, t)$ , allows for any tectonic contributions to sea level. Many reefs occur in areas of tectonic uplift or subsidence and the separation of these effects from the isostatic signals remains a major challenge. A frequently used criterion is to examine whether there is evidence for a fossil Last Interglacial reef at the same location. If this occurs within a few meters of present sea level, then the site can be considered to have long-term tectonic stability to better than 0.1 mm/year. Alternatively, if the sea-level behavior can be calibrated against sites of known tectonic stability, the comparison of model predictions and observations establishes rates of tectonic uplift or subsidence.

The fourth term,  $\Delta\zeta_{\text{O}}(\varphi, t)$ , includes any oceanographic or meteorological factors that cause sea level to depart from a long-term equipotential surface. These are generally treated as perturbations in high-resolution analyses of recent and Holocene sea-level change.

Despite most modern coral reefs occurring far from the ice margins of the last glaciation – far-field sites – both components of the isostatic response occur. The glacio-isostatic response here is characterized by a broad wavelength response, reflecting global-scale mantle flow driven by the growth and decay of the large ice sheets, and the sea-level response is not sensitive to the details of the ice sheets. More important here is the hydro-isostatic component and this is strongly dependent on the changes in the distribution of water around the site.

Figure 2 illustrates sea-level change at a continental margin site. At a time  $t$ , the land surface is at  $a - a'$  and the shoreline is at  $A(t)$ . Between  $t$  and the present,  $t_{\text{p}}$ , land uplift has occurred by an amount  $u_{\text{r}}$  and the new land surface is at  $b - b'$ . The ocean volume has also increased so as to raise the ocean level relative to the center of mass of the earth from  $\zeta_{\text{A}}$  to  $\zeta_{\text{B}}$  and the present shoreline is at  $B(t_{\text{p}})$ . The original shoreline will now occur at  $A'$ , at  $\Delta\zeta(t)$  below the present sea level. The relative sea-level change is therefore

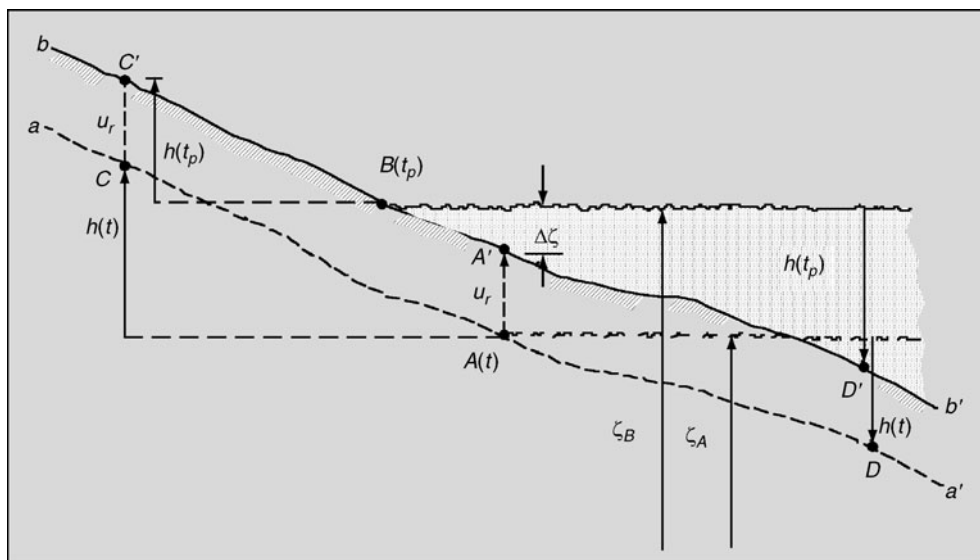
$$\Delta\zeta(t) = (\zeta_{\text{A}} - \zeta_{\text{B}}) - u_{\text{r}}$$

and the change in elevation of any point (e.g., from  $C$  to  $C'$  on land or from  $D$  to  $D'$  offshore) measured with respect to the sea level of the epoch is

$$h(t) = h(t_{\text{p}}) - [(\zeta_{\text{A}} - \zeta_{\text{B}}) - u_{\text{r}}] = h(t_{\text{p}}) - \Delta\zeta(t)$$

This formulation is independent of the cause of land movement or ocean volume change but for the glacio-hydro-isostatic contribution only, the land movement component will depend on the response of the earth's surface to the changing ice–water load and the displacement of the ocean surface will depend on how any meltwater is distributed into the ocean basins and on the changing gravitational attraction of the solid earth and the ice on the water surface. In the case of glacio-hydro isostasy  $u_{\text{r}}$  and the radial displacement of the ocean surface ( $\zeta_{\text{A}} - \zeta_{\text{B}}$ ).





**Glacio-Hydro Isostasy, Figure 2** Schematic representation of relative sea-level change  $\Delta\zeta$  in an environment of land uplift  $u_r$  and a rise in the radial distance of the ocean surface ( $\zeta_A - \zeta_B$ ). (See text for details).

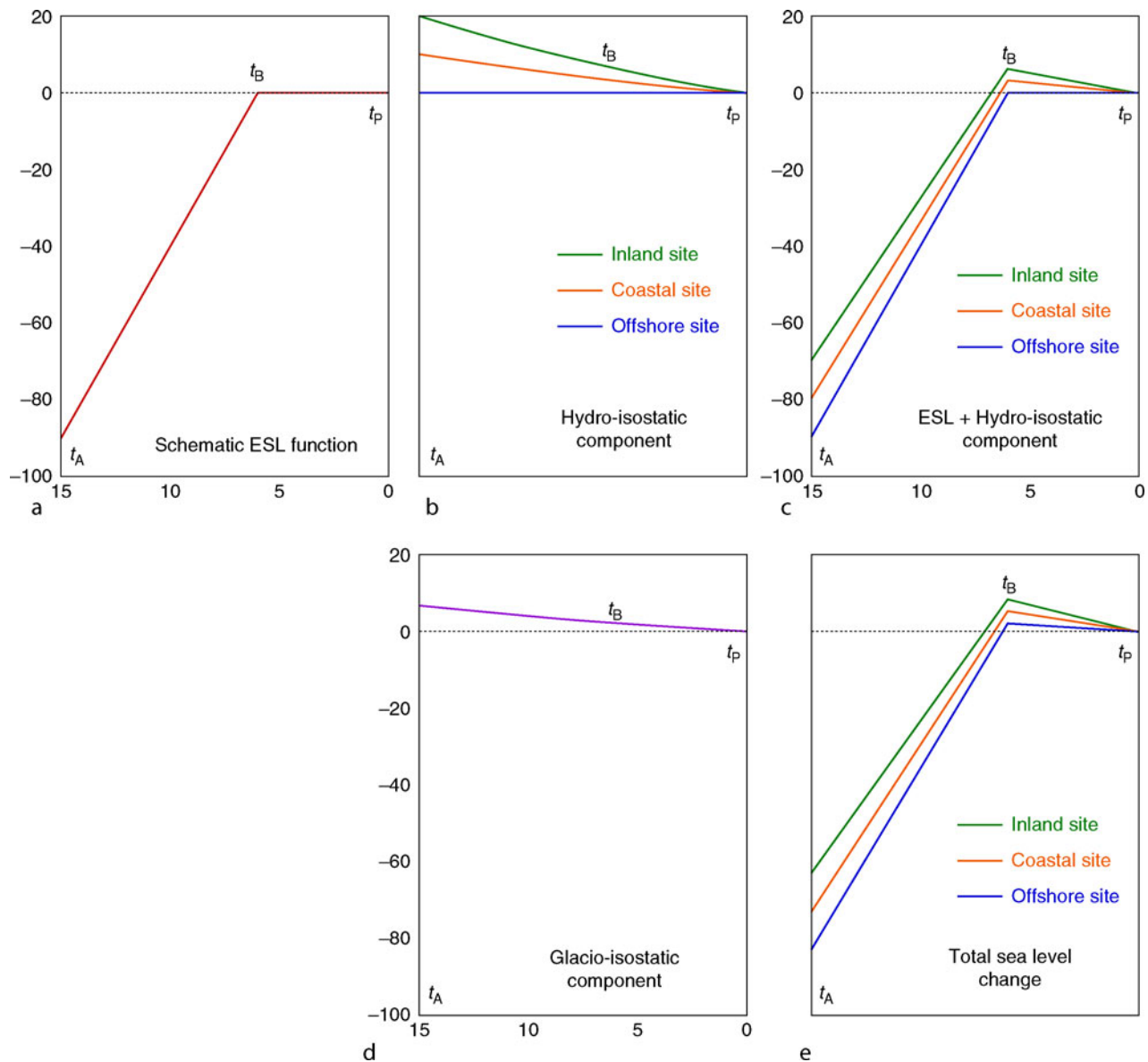
Consider the following simple model. At the end of a long glacial period,  $t_A$ , a volume of ice has been added rapidly into the ocean at a constant rate until a time  $t_B$ . The ocean volume then remains constant until the present  $t_P$  (Figure 3a). During the deglaciation the meltwater loads the ocean floor and induces flow in the mantle away from the areas of loading to beneath the continents and to compensate for the concomitant rebound beneath the ice sheets. The resulting subsidence of the seafloor will include an elastic response followed by a viscous response that continues after the load has stabilized and will still occur today. The ocean has to fill the void created by the subsiding seafloor and the sea surface, in a first approximation, follows the seafloor. In the middle of the ocean basins, the maximum subsidence can be roughly approximated by the local isostatic effect. At the continental margin, because the water loading occurs to one side only, the subsidence will be about 50% of that in mid-ocean, largely because of the flexural strength of the lithosphere. At far-offshore island sites, there is no change because the island subsides with the seafloor. Inland from the coast, within a deeply indented gulf, for example, where the crust is being progressively dragged down less by the ocean load, this change will approach  $u_r$  (Figure 3b).

The resulting spatial variability in the hydro-isostatic response will then have the following characteristics (Figure 3c):

- A small amplitude highstand near the coast with a maximum at the time meltwater addition ceased and with a magnitude that depends on the distance from the coast.
- A rise of sea level prior to the maximum highstand that occurs later with distance from the coast.

- Relative sea level at the LGM that varies across the shelf and that approaches the ice-volume equivalent value at some distance from the coast.

This scenario is an incomplete description of the relative sea-level change across the continental shelf since the glacio-isostatic contribution has been ignored, as has the change in gravitational potential during the deglaciation and subsequent relaxation phase and any change in water load caused by the migration of shorelines during the sea-level rise. Of these neglects the most important one is the glacio-isostatic factor, including the gravitational part. At the time of maximum glaciation a broad deformational bulge develops around the ice sheet and this slowly subsides during and after the deglaciation phase. When this bulge occurs in an ocean environment, additional space is created that draws water into it and away from the far-field locations where the glacio-isostatic signal becomes one of a falling sea level (Figure 3d). This contribution varies relatively slowly across the far field and the predominant spatial variability across a reef system will come from the hydro isostasy. The combined effect at the far-field sites is that a small amplitude highstand will also occur for many ocean island sites (Figure 3e). It is sometimes stated that ocean islands act as dipsticks and provide a direct measure of the changes in ocean volume. But this is a first approximation and in reality this occurs only at a few sites where the combination of all the factors contributing to the isostatic perturbation cancels out. These simple illustrations also point to a second common misconception, that it is the loading of the shelves that constitutes the hydro-isostatic correction. But this is one part of the water load only and the principal part comes from the long-wavelength load of the entire ocean floor.



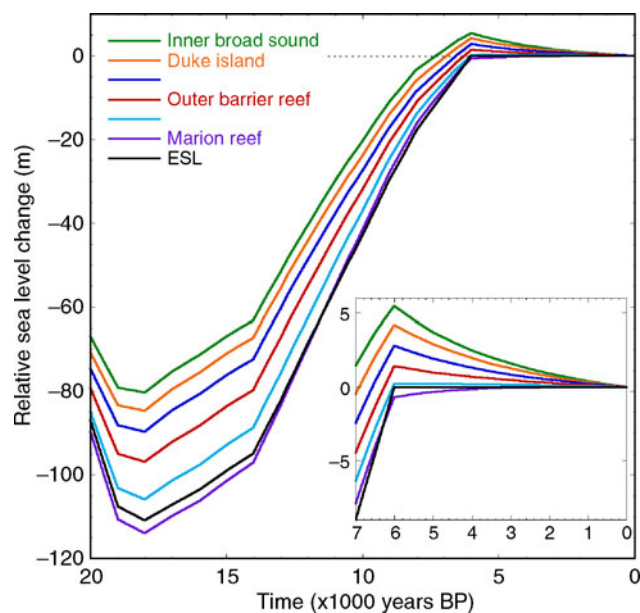
**Glacio-Hydro Isostasy, Figure 3** Schematic components of the contributions to relative sea level at far-field sites across a continental margin. (a) The ice-volume equivalent sea-level (ESL) component. (b) The hydro-isostatic component at three locations across the margin. The inland site would correspond, for example, to the head of a deeply indented gulf. (c) The combined ESL and hydro-isostatic contributions. (d) The glacio-hydro-isostatic contribution at the far-field locations. This part varies only slowly across the area. (e) The total glacio-hydro-isostatic change in sea level.

### Some examples

Figure 4 illustrates predictions based on the complete theory, for sites equidistantly spaced across the Great Barrier Reef (Queensland, Australia) from within the inner Broad Sound, across the outer Reef and to Marion Reef in the Coral Sea. They are based on nominal ice and earth models that have been found to describe well the far-field behavior of sea level during Holocene time and are representative of a wide range of plausible models. In this model calculation, it has been assumed that all melting

ceased abruptly at 6,000 ( $C^{14}$ ) years BP and this results in the sharp highstand at this time. If this cessation was less abrupt then this peak becomes broader and its shape is diagnostic of changes in late Holocene ocean volumes. This example illustrates that with increasing distance from the continental coastline:

- the mid-Holocene highstand decreases in amplitude from a few meters maximum at the ‘inland’ sites;
- the oldest corals occurring at sea level become increasingly younger;

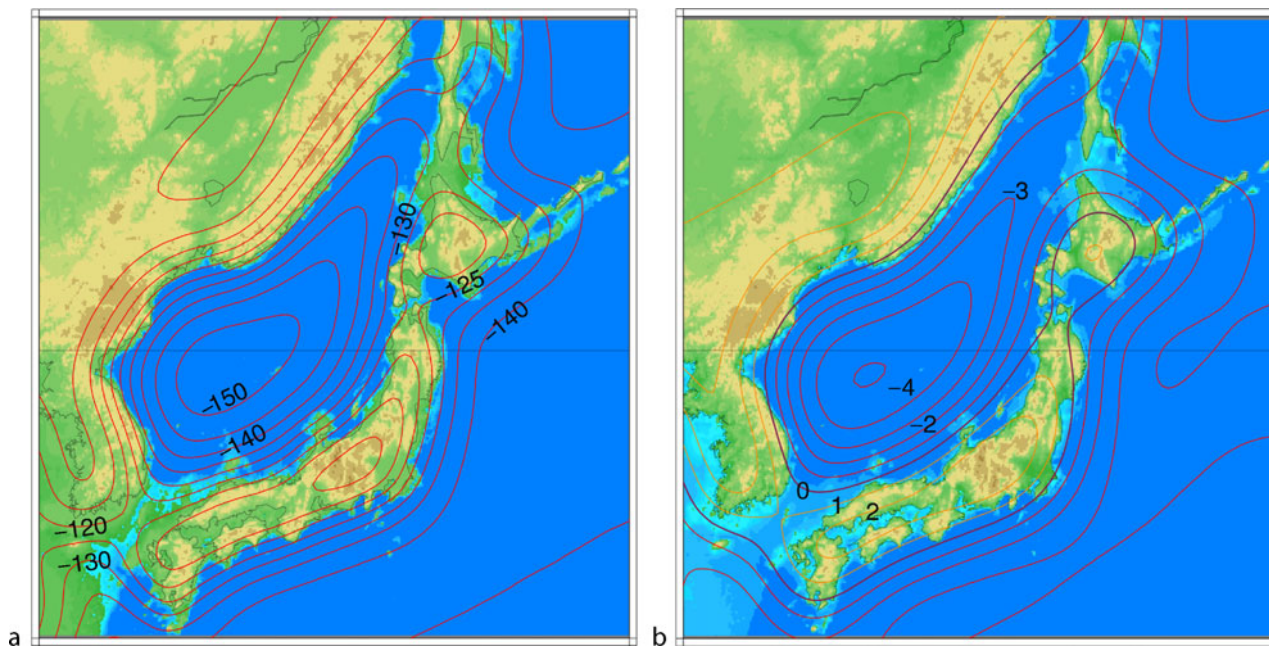


**Glacio-Hydro Isostasy, Figure 4** Predicted sea-level change for the complete glacio-hydro-isostatic rebound along a section at a spacing of ~35 km across the Great Barrier Reef (Australia) from the inner side of Broad Sound to Marion Reef within the Coral Sea. These results are for nominal earth parameters and ice sheets that cease all melting at 6,000  $^{14}\text{C}$  years before present.

- the pre-mid Holocene rise in sea level increasingly lags the globally averaged sea-level rise; and
- the Last Glacial Maximum sea levels increase in depth.

Across the Great Barrier Reef, adjacent islands and continental shoreline, the observational evidence generally confirms these trends although it has not always been interpreted in terms of the differential isostatic response. For example, the observation of a progressive decrease with distance from the shore of the oldest coral ages found at the upper limits of growth, has sometimes been interpreted as a result of outer reefs being less capable of keeping up with sea-level rise than inner reefs.

The amplitudes of the highstand and the lags in the response are dependent on the rheological parameters describing the earth's mantle and lithosphere so that the matching of observations and predictions enables these parameters to be estimated for the region of analysis. Glacio-hydro-isostatic studies of the formerly glaciated (near-field) regions likewise provide information on the earth's response function as well as on the dimensions and timing of the former ice sheets, particularly during their final decay phase. By an iterative process between far- and near-field regions, it becomes possible to separate the earth- and ice-model parameters that quantify the rebound formulation and thus to develop a predictive global model for that part of sea-level change associated with the glacial cycles. These models are best developed



**Glacio-Hydro Isostasy, Figure 5** Glacio-hydro-isostatic sea-level variation across the Japan Sea and adjacent areas at two epochs. (a) 20,000 (cal) years before present, at the time of the maximum glaciation. The contour interval is 5 m. (b) 7,000 (cal) years before present, at the time of the mid-Holocene highstand formation. The contour interval for sea-level change is 1 m. The red contours are negative and the orange contours are positive.



for the interval after the last glacial maximum but they have also been extended to earlier periods, particularly the Last Interglacial. In the context of coral reefs from this latter period, it is important to recognize that these isostatic processes also occur and that the elevations of Last Interglacial sea levels will exhibit similar patterns of spatial variability.

Figure 5 illustrates the predicted spatial variability for one region, the Japan Sea, that, in the absence of tectonics, is representative of most far-field regions. The results are for two epochs, the time of the last glacial maximum (LGM) and the time of the mid-Holocene highstand but the spatial variability is similar for all other epochs. Thus, even within relatively small regions sea level cannot be represented by a single curve. At the LGM the predicted sea levels vary by ~30 m, being significantly shallower in the Korea Strait, for example, than in the middle of the Japan Sea where it exceeds the ESL value. Likewise, the Holocene highstand amplitudes are predicted to occur up to 2 m above sea level in some locations but not in northern Hokkaido or the Kurile Islands.

## Conclusion

The phenomenon of glacio-hydro isostasy means that even in the absence of vertical tectonics, sea level at any time is spatially variable, that it can be rising in one location while falling elsewhere. This variability is a consequence of the earth's deformation under the changing load and to the changes in the gravity field. The mapping of this variability therefore provides information on both the earth's rheology and on the history of the ice sheets. But it also needs to be known if sea level is used as a reference for vertical tectonics or, for example, if reef response to changing sea level is to be investigated. The theory and implementation of the glacio-hydro-isostasy theory is sufficiently well developed for it to provide a sound basis for interpolating between the limited sea-level observations for the time since maximum glaciation and for reconstructing paleo shorelines and water depths.

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## Cross-references

Last Glacial Lowstand and Shelf Exposure  
Sea Level Change and Its Effect on Reef Growth  
Volcanic Loading and Isostasy

## GLOBAL OCEAN CIRCULATION AND CORAL REEFS

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## Synonyms

Global scale currents

## Definition

Ocean circulation denotes ocean-scale current systems that change seasonally but persist from one year to the next.

## Introduction

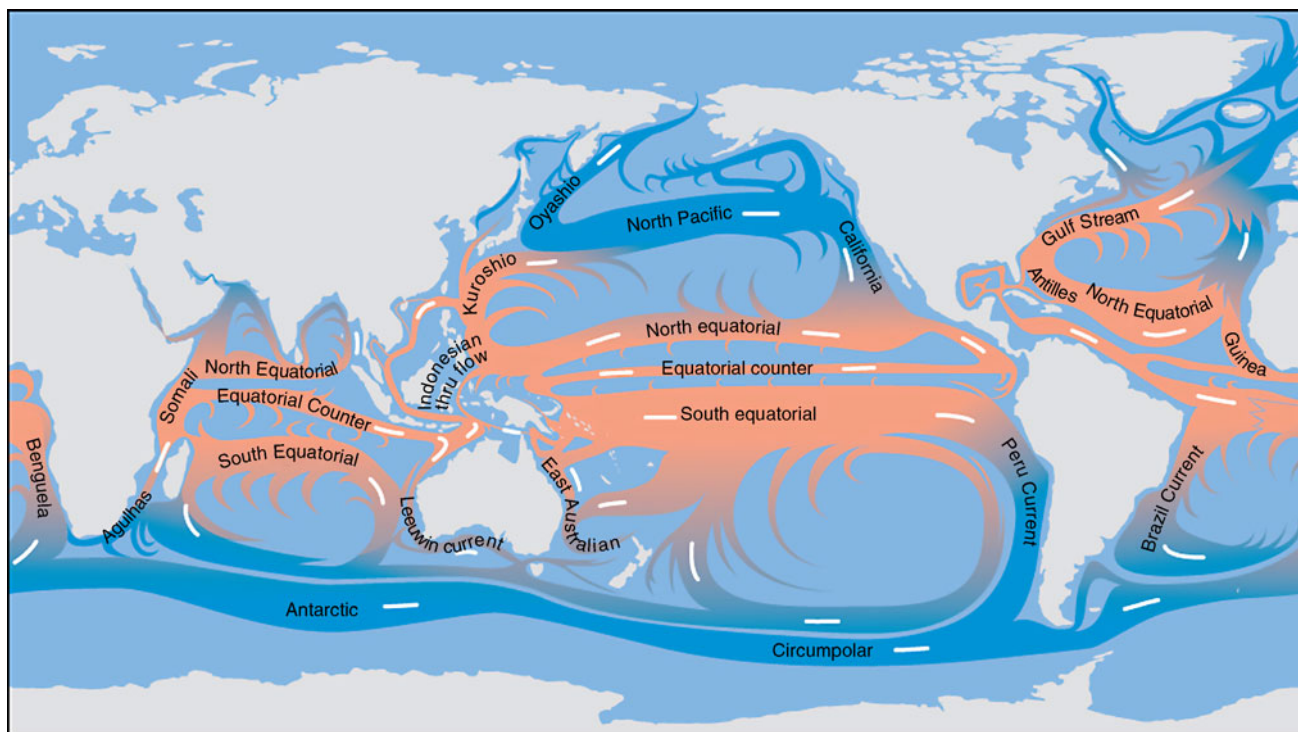
Reefs develop in most parts of the world where reef-building (zooxanthellate) corals grow and where the ocean is warm. This geographic template is created by the world's great ocean currents (Figure 1). Currents therefore play a key role in the geographic extent of reef formation as well as in the dispersal of reef biota. They are also critical determinants of the pathways of species evolution.

The historical role of ocean circulations as drivers of reef and faunal distributions is closely linked to other drivers, not only temperature but also sea-levels and the configuration of the continents. Two very different scales – global and regional – operate simultaneously. Global scales over geological time provide the template of both coral reef distributions and zooxanthellate coral distribution. Regional scales over millennia or less control details of the distributions of corals and have a short-term, ecologically driven influence on reef development (see below).

## Origins of modern circulation patterns

At the start of the Cenozoic Era, ocean circulations were dominated by a circum-global equatorial path via the Tethys Sea and Central American Seaway. There was no circulation around Antarctica (the remnants of Gondwana) and all oceans were warm and sluggish, with no strong latitudinal temperature gradients as we have today. This pattern persisted until South America rifted free of Antarctica during the Late Eocene–Early Oligocene 40–35 million years ago (mya), and Drake Passage opened. At this point, for the first time since Gondwana formed, the Southern Ocean began circulating around Antarctica, moving eastward in response to the direction of rotation of the Earth and checked only by the coastlines of the three southern continents.

The formation of the Antarctic Circumpolar Current was the critical event that gave birth to modern circulation patterns. Where the three continents of South America, Africa, and (to a lesser extent) Australia project into its path, cold water is deflected north along the western margin of each continent. The currents then move westward in the tropics where they are warmed, and return south along



**Global Ocean Circulation and Coral Reefs, Figure 1** The global pattern of ocean circulation (after Veron, 2000).

the eastern side of each continent. These three anticlockwise circulations of the Southern Hemisphere oceans are in turn linked to clockwise circulations in the Northern Hemisphere in latitudinally zoned gyres (Figure 1). In effect, the opening of Drake Passage allowed the sluggish tropical circulations of the early Cenozoic to be replaced with stronger circulations, powered by the Antarctic Circumpolar Current, creating the latitudinal temperature gradients of today. It also formed an insulating blanket around Antarctica causing, at the time of formation, the surface temperature of the Southern Ocean to plunge by 10–15°C (Frakes et al., 1992).

During the latter half of the Cenozoic, there were two fundamental modifications to this pattern (Adams, 1981). The first was the widening of the North Atlantic, as, until this happened, the North Atlantic did not regulate global climates via the Ocean Conveyor and Gulf Stream as it now does. The second was the progressive reduction in size of the Tethys Sea. The Tethys, the evolutionary cradle of most tropical marine life, waxed and waned throughout the Early to Middle Cenozoic according to continental movements and sea-level changes, to be finally choked off during the Late Miocene (10 mya), a process which severed all tropical connection between the Atlantic and Indian Ocean (Figure 2).

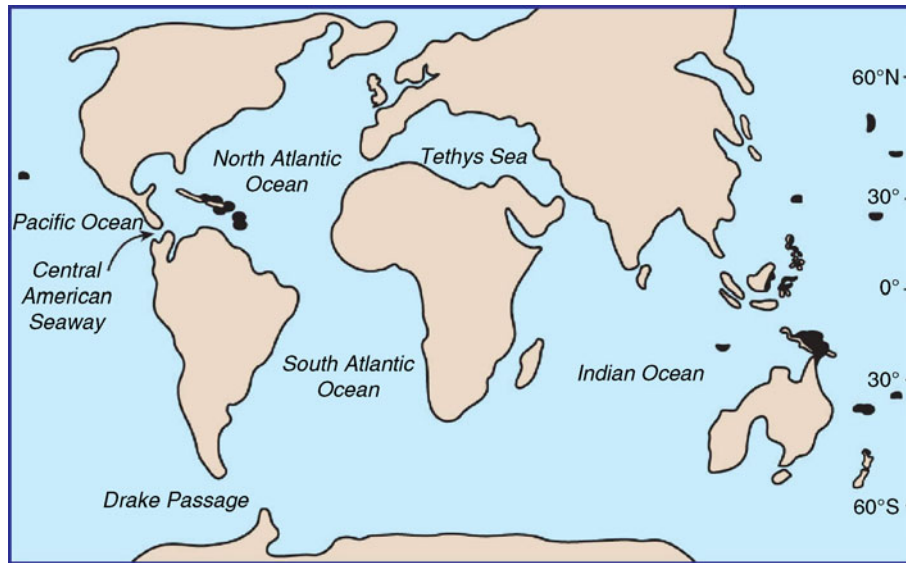
There was one final event crucial to ocean circulation before Ice Age cycles took control: the formation of the Isthmus of Panama in place of the old Central American Seaway. This was a gradual process completed in

3.4 mya (Coates et al., 1992), which greatly enhanced the flow of the Ocean Conveyor to the North Atlantic (Burton et al., 1997) and allowed El Niño Southern Oscillation cycles to establish.

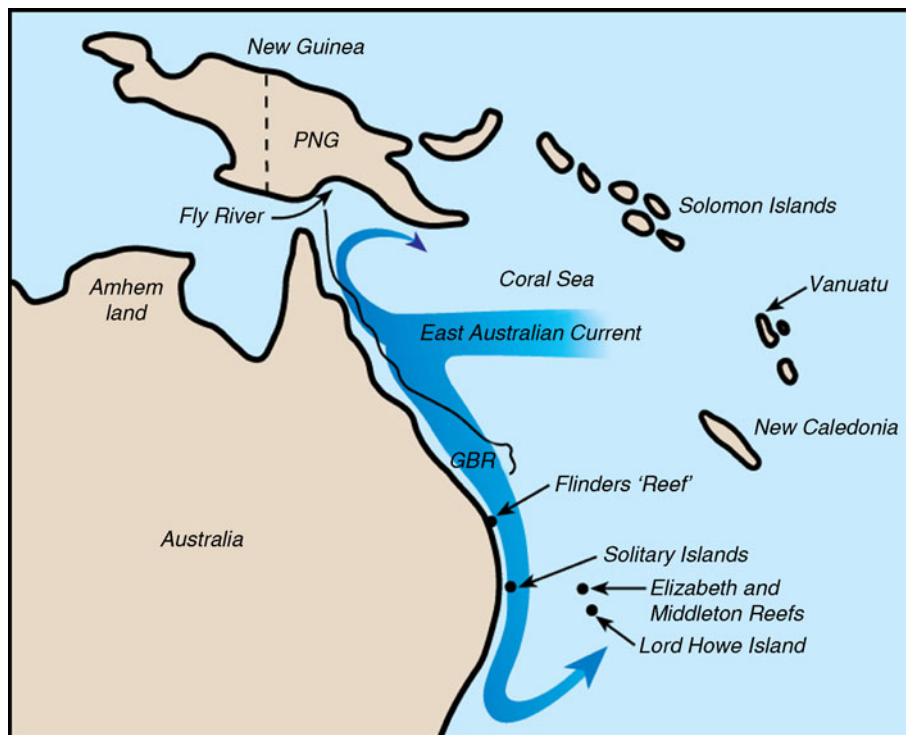
### Ocean circulation and biogeographic patterns

The distribution of corals and reefs during the Early Cenozoic essentially involved a transfer of biodiversity from the Old World of the Tethys Sea to the New World of the Caribbean and Central American Seaway. Through this process, coral diversity around the Central American Seaway reached a peak during the Oligocene and extensive reef development also spread throughout the central Indo-West Pacific, which had become clearly distinct from the Tethys.

By Early Miocene, the distribution of reefs was similar to that of today, with the major exception of the Tethys Sea which was held open only by a narrow passage between the Indian Ocean and proto-Mediterranean (Figure 2). The biogeographic patterns of corals at this time is unknown, but by then the Indo-West Pacific had inherited much of the diversity that had originally evolved in the Tethys and Caribbean (Veron, 1995). The Miocene ended 5.3 mya with the extinction of the last remnants of the ancient fauna of the Tethys. Late Miocene reef remains are very common in the western tropical Pacific (Kiessling and Flügel, 2002), with outcrops extending as far south as New Zealand (Hayward, 1977).



**Global Ocean Circulation and Coral Reefs, Figure 2** Positions of the continents during the Middle Miocene (around 15 mya). Extensive reef remains (in black) are scattered around the world and as far south as New Zealand (after Veron, 2008).



**Global Ocean Circulation and Coral Reefs, Figure 3** The role of poleward currents in latitudinal reef distribution along eastern Australia. The East Australian Current disperses coral larvae to the world's highest latitude atolls (Elizabeth and Middleton Reefs) and highest latitude reef (Lord Howe Island). South of the Great Barrier Reef, there are abundant corals but no reef development at the few shallow coastal localities – Flinders Reef (a sandstone outcrop) and the Solitary Islands – due to temperature and other environmental constraints (after Veron, 2000).



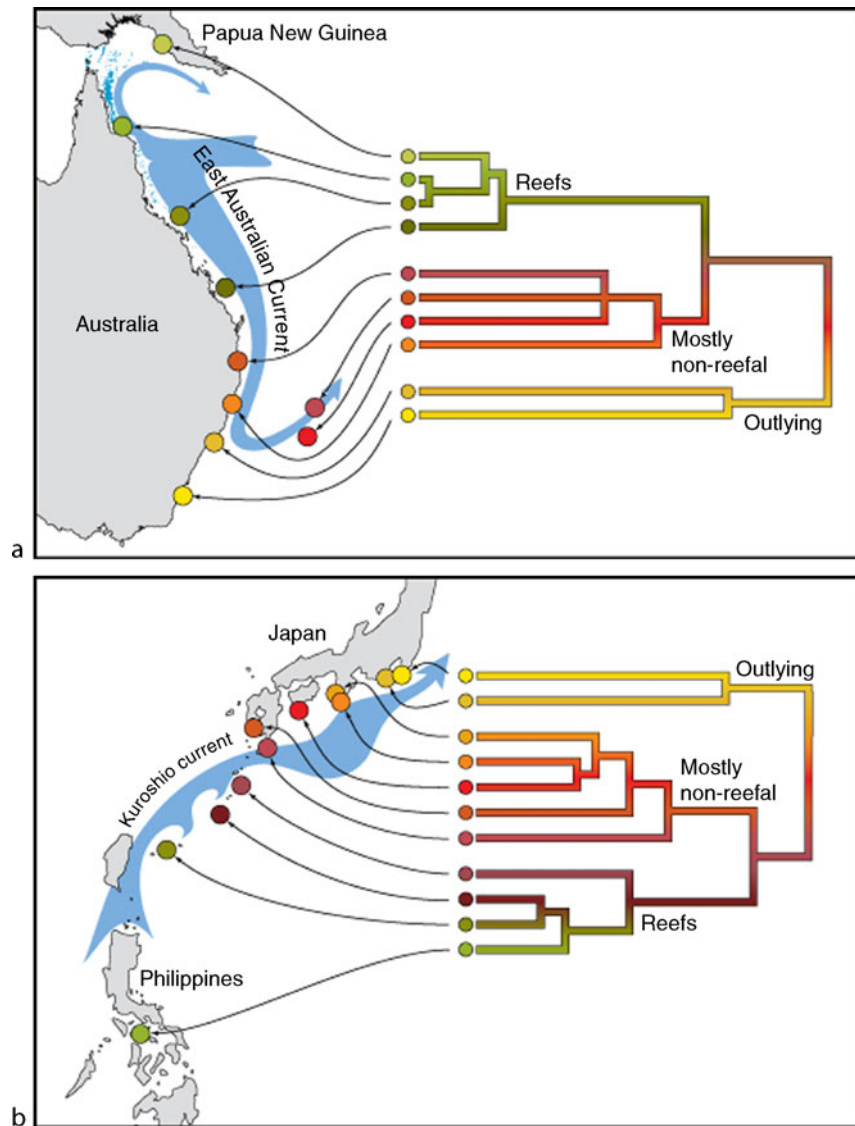
At this time, corals had yet to undergo one more major change in their global pattern of diversity. Throughout much of the Miocene (24–5.3 mya), but certainly by the Late Miocene, the eastern Atlantic had become too cold for reef corals as a result of the cold current plying along the west African coast (Esteban, 1980). The Atlantic thus became an isolating barrier separating the Caribbean from the Tethys where once it was a corridor.

### Ocean circulation and reef formation

It is only at oceanwide scales that there is only a clear correlation between the distribution of corals and the distribution of reefs, although surface currents play a dominant

role in both. The essential reason is that good reef development can occur in regions of low coral diversity: reef formation does not depend on a high coral diversity (Glynn et al., 1996).

With rare exceptions (carbonate platforms built by vermetid molluscs, serpulid worms, and non-scleractinian corals), the presence of zooxanthellate corals is essential for reef development. Thus, the oceanographic history of any major part of the world, as described above, determines the gross pattern of both reef development and zooxanthellate coral occurrence. Both require shallow substrata, minimal quantities of mud of terrestrial origin, high light levels, high salinity, a suitable temperature regime, and  $\Omega_{\text{aragonite}}$  of 3.8 or higher (see



**Global Ocean Circulation and Coral Reefs, Figure 4** The role of surface currents in dispersal of corals along the eastern Australian coast (a) and the islands of Japan (b). Dendrograms show similarity of species composition occurring at each site indicated. These include reef communities, non-reef communities, and outlying regions (after Veron, 1995).

Chapter “Corals – environmental controls on growth”). Of these constraints, all but temperature applies equally to corals and reefs on regional scales.

Temperature is more limiting for reefs than corals because of an ecological constraint: most corals can tolerate temperatures as low as 14°C for extended periods, but consolidated reefs will not accrete under 18°C because at that temperature corals cease to be competitive with macro-algae in most parts of the world (Veron and Minchin, 1992). Along subtropical continental coastlines where at least some zooxanthellate corals occur, reefs extend to a latitudinal limit defined by temperature which, in turn, is controlled by the strength of poleward currents (for example, Figure 3). In open oceans remote from continents, the same constraint applies where suitable substrates exist, but as poleward currents are weaker, the latitudinal extent of reef development is less.

One further aspect of the role of temperature in controlling the latitudinal range of reefs is that reefs can develop episodically, surviving as geological structures during intervals of emergence and cold (such as were created by the glacial cycles of the Pleistocene) and growing during interglacial warm intervals.

### Surface currents and dispersal

There is a wealth of information from experiments, genetics, taxonomy, and biogeography that coral larvae are able to make very long ocean journeys, some enduring weeks, even months, on the sea surface before settling (Richmond, 1987). Species endurance therefore depends on the speed and direction of currents as well as the existence of suitable substrates.

Survival during these voyages depends on time, therefore on the distance traveled, and speed.

Corals are dispersed along continental coastlines of eastern and western Australia by the East Australian Current and Leeuwin Current (respectively) in the Southern Hemisphere and along the islands of Japan in the north by the Kuroshio. In each case, there is an orderly

“drop-out” sequence where species numbers progressively attenuate (Veron, 1995). Each of these boundary currents varies in position and strength, each variation potentially causing changes in the number and variety of propagules reaching high-latitude reefs. Importantly, as each current flows poleward, propagules entrapped in them are on non-return journeys. As a result, these currents overwhelmingly dominate the nature and diversity of coral communities found today (Figures 3, 4a, b; Harriott and Banks, 2002).

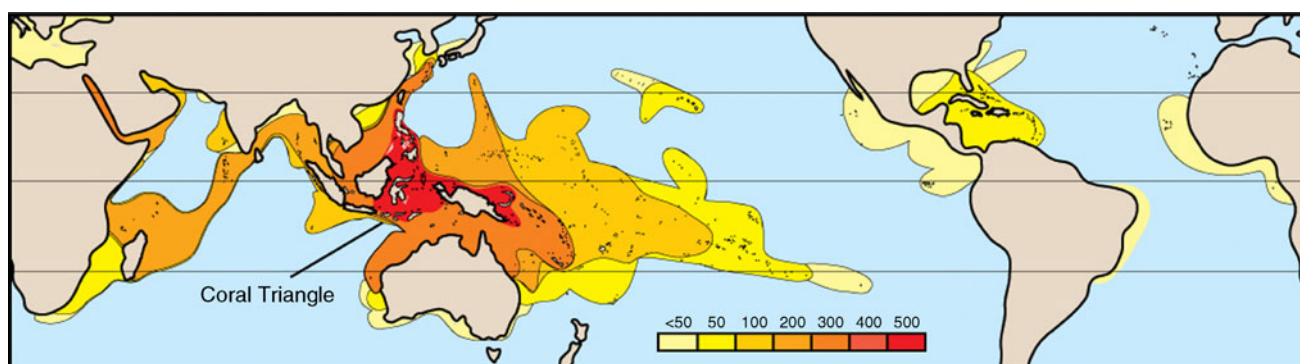
Surface currents also play a part in defining the global center of coral diversity, the so-called “Coral Triangle” (see Chapter “*East Indies Triangle of Biodiversity*”; Figure 5).

There are multiple reasons why the Coral Triangle should be so diverse relative to other reef regions (Veron et al., 2009): (1) The Coral Triangle acts as a ‘catch-all’ for larvae moving *towards* the region, entrained in both the South Equatorial Current and the North Equatorial Current (Jokiel and Martinelli, 1992; Veron, 1995). (2) Dispersion occurs *away* from the Coral Triangle leaving that region biodiverse relative to other regions where attenuation has occurred. (3) Complex eddies created by the Indonesian Through-flow (Gordon and Fine, 1996) drive genetic mixing which constantly changes with wind, season, and (over geological time) sea level. Genetic mixing of this nature creates genetic heterogeneity through vicariance and reticulate evolution.

### Ocean circulation and evolution

Evolution in corals is exceedingly slow, whereas long-distance dispersal can be rapid – even within the time of a single generation. The two processes are therefore only tentatively linked, not only because of time but also because genetic pathways are constantly changed by variations in ocean currents.

The distance traveled by coral larvae and probably that of most other major invertebrate taxa can indeed be so vast that the majority of species found in, for example, the Great Barrier Reef also occur within the Coral Triangle



**Global Ocean Circulation and Coral Reefs, Figure 5** Contours of coral diversity (species richness). Species disperse from regions of high diversity, notably the Coral Triangle, to other Indo-Pacific regions. Many regions of the world, including most of the Atlantic (but not the Caribbean) and far eastern Pacific, have few, if any, corals and no reefs. However, over distances of a thousand kilometers, the occurrence of both corals and reefs is highly predictable (after Veron, 2008).

and a high proportion are even recognizable as far away as the Red Sea.

The relative strength and direction of the currents and the endurance of the larvae are key aspects of these spatial patterns – not just the patterns of today, but those of all times past, for as long as these species have existed. Today, most major currents are generally stable and move in predictable directions. However, over geological time, these same currents have changed their strengths and directions repeatedly. This has created changing geographic patterns of genetic mixing quite unlike genetic pathways normally found on land. The result, over geological time, is a template of constant change, which in turn is the mechanism that drives reticulate evolution (see Chapter *Scleractinia, Evolution and Taxonomy*).

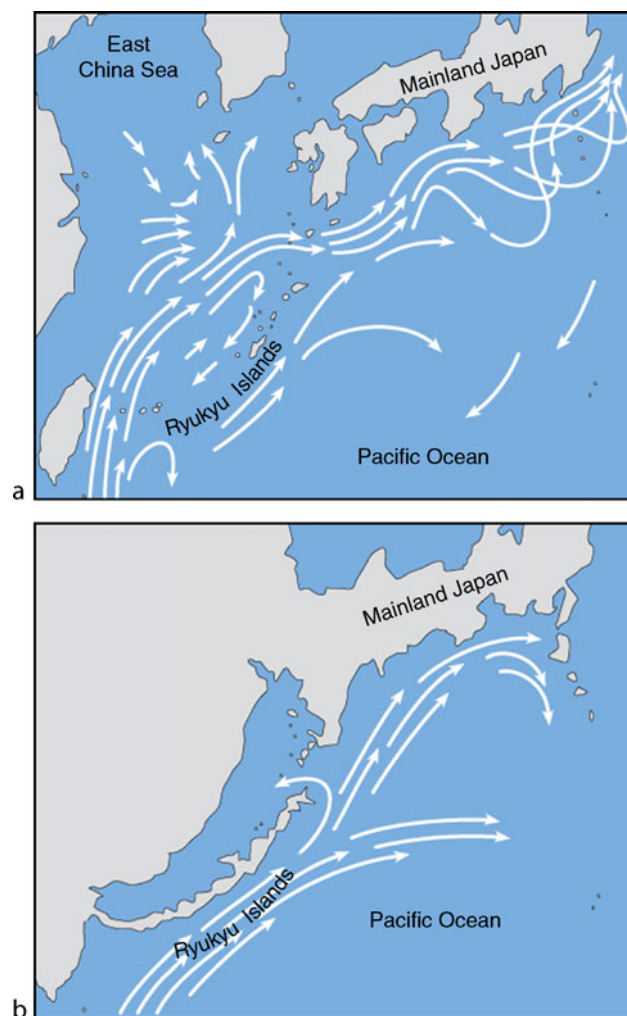
The Kuroshio, the world's strongest continental boundary current, well illustrates change over time in both strength and direction. In historical time (decades to centuries), this current has repeatedly changed its path south of mainland Japan (Figure 6a), each time causing major redistributions of benthic fauna as well as local extinctions. Over geological intervals of 100,000s of years, combinations of glacial sea-level changes and tectonic uplifts have created enormous changes to the Japanese coastline and, consequently, the path of the Kuroshio (Figure 6b). Variations between these two extremes not only produced changes in distribution and diversity of most marine biota but also changes in their genetic compositions (Figure 6).

### Meso- and microscale circulation and environments

Most marine life undergoes dispersion, either long-distance (noted above) or within single reefs during larval stages in their life cycles, and most benthic and neritic life becomes established on particular areas of reef according to local environmental cues. At these mesoscales, currents are also the conveyors of food for filter – and detritus – feeding taxa, and oxygen and nutrients for all taxa. At yet finer scales, currents (generated by tides and waves) determine the growth form of branching corals and thereby the three-dimensional nature of most types of shallow reef habitats. These aspects of ocean currents are outside the scope of this article.

### Summary

The global distribution of reefs is a product of the major patterns of ocean circulation that have existed since Early Cenozoic which, in turn, were dependent on continental movements. Reef distributions are also controlled by the presence or absence of reef-building corals and therefore the physical parameters which control the growth of zooxanthellate corals. Of these, temperature is critical, the lower boundary of which is different for reefs and corals. Currents are also the pathways of dispersal of most marine taxa and are thus the principal drivers of evolutionary change. On finer scales, currents are an intimate part of reef ecological processes and morphologies.



**Global Ocean Circulation and Coral Reefs, Figure 6** Changing ocean circulation patterns of the Kuroshio. Over historical times (a), major changes have occurred in the path of the Kuroshio south of mainland Japan. Some of these are seen in fossil coral outcrops (arrowed). Over 100,000s years, the coastline has changed radically from sea-level changes and tectonic uplift, creating far greater changes to the Kuroshio (after Kimura, 1991). Variations between these extremes have created a constantly changing template for evolutionary change.

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## Cross-references

[Corals: Environmental Controls on Growth](#)  
[Scleractinia, Evolution and Taxonomy](#)  
[East Indies Triangle of Biodiversity](#)  
[Lagoon Circulation](#)  
[Tethys Ocean](#)  
[Reef Interconnectivity/Larval Dispersal](#)

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## GREAT BARRIER REEF COMMITTEE

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In 1922, the Queensland branch of the Royal Geographical Society of Australia set up the Great Barrier Reef Committee following an address to the Society by the Professor of Geology and Mineralogy at the University of Queensland, Henry Richards. The address, entitled “Problems of the Great Barrier Reef” highlighted the need for scientific investigation of the Reef and followed a visit by Richards to America to attend the Pan-Pacific Scientific Conference where, among others, he met W.M. Davis (Hill, 1985a, b; Jones, 1974; Bowen and Bowen, 2002).

Membership of the Committee was through invited nominations from the Government and Academic institutions in Australia and elsewhere. However, disagreements with the parent body, the Royal Geographical Society led to a separation of the Committee in 1924 although it incongruously maintained the title of Committee. Initial funding came from the Queensland Government and Universities of Sydney and Queensland and further valuable support came from the provision of places on survey vessels of the fledgling Australian Navy and the Commonwealth steamer that serviced the many lighthouses on the reefs and islands.

Early research was much influenced by Richards’ geological background with, for example, Sydney University graduates undertaking work into coastal landforms and sea level, published in the independent Transactions of the Great Barrier Reef Committee. However, Richards had larger targets in mind including investigations into the foundations of the Reef to see if Darwinian type subsidence was applicable. In 1926, a hole was drilled to 180 m on Michaelmas Cay, and in 1937 further drilling on Heron Island to 240 m was undertaken. Results were inconclusive as to the proving or otherwise of the nineteenth century hypotheses of Darwin, Dana, and others but did provide useful information, which was being quoted even 50 years later (e.g., Lloyd, 1973).

Another early aim of the Committee was to set up a research station on one of the reef islands but as this was not immediately possible, an alternative strategy was adopted and that was to promote an expedition based on a reef island for at least one full cycle of seasons. Discussions were held with various scientific bodies, especially in England and support came especially from the British Association for the Advancement of Science. The cay on Low Isles, north of Cairns, was the chosen site where 23 scientists were based under the leadership of (Sir) Maurice Yonge in 1928–1929. A variety of studies, including zoological, botanical, sedimentological etc., were undertaken and the large number of reports were published by the British Museum of Natural History. They have remained the basis for coral reef research ever since.

In addition to the main expedition, the Royal Geographical Society supported a smaller study of mainly islands of the southern half of the Great Barrier Reef (GBR). This was led by Professor J.A. Steers of Cambridge University and accompanied by Michael Spender and was followed by a second 4-month expedition mainly to previously unvisited islands of the Reef in 1936. Their results were published in the Geographical Journal and Reports of the Great Barrier Reef Committee (Steers, 1929, 1937, 1938; Spender, 1930). This work did much to highlight the value of reef islands as a source of geomorphological information on coral reefs and established Cambridge University’s Geography Department as a source of reef researchers.

Establishment of a permanent research station on the GBR was not possible until after World War II. Initially a relatively small facility, it was set up in 1951 on Heron

Island at the southern end of the GBR and close to the capital city of Brisbane. This has subsequently become one of the major reef research facilities in the world.

During the second half of the twentieth century, the Committee was very active in conservation issues of the GBR, something which Richards had originally seen as being important. Scientific evidence about the crown-of-thorns starfish and oil drilling on the Reef, and the need to create the Great Barrier Reef Marine Park Authority was presented to a number of government commissions.

The Committee also played a part in the organization of the Second International Coral Reef Symposium in 1973, which uniquely was held aboard the cruise ship "Marco Polo" travelling from Brisbane to Lizard Island and return. Also in the same year, the Committee was involved in the organization of a further expedition to the northern GBR. Enthusiastic support came from Sir Maurice Yonge and Professor Alfred Steers from the 1928–1929 expedition. Major input came from the Royal Society of London and from the Universities of Queensland (Queensland University and the new James Cook University of North Queensland). The leader of the expedition was Dr. David Stoddart of Cambridge University. Again, significant data was obtained especially from the reef islands and comparison with results from 1928–1929 to 1936 allowed some assessment of the dynamics of the islands. Results of this work were published in 1978 in the *Philosophical Transactions of the Royal Society*, London A, 291 and B, 184.

In 1988, after 66 years as an unattached committee with nominated membership, the Great Barrier Reef Committee became the Australian Coral Reef Society (ACRS) with subscription membership. However, continuity is recognized and this makes it the oldest organization concerned with coral reefs in the world.

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## GREAT BARRIER REEF: ORIGIN, EVOLUTION, AND MODERN DEVELOPMENT

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## Introduction

The Great Barrier Reef (GBR) is arguably the largest coral reef system to have ever existed on the planet. It lies off the northeast Australian margin – a passive margin, but a margin which is being gradually consumed as a consequence of Australia's inexorable drift toward the New Guinea foreland basin and the trenches to the north. Unless plate motions change, the Great Barrier Reef is a temporary acquisition. The following is the story of its development to date – one of three major reef systems to have existed in the region since the Miocene, and the Great Barrier Reef owes its existence to both its predecessors.

## The architecture of offshore northeast Australia

The northeast Australian margin ([Figure 1a](#)) comprises the continental shelf and a number of marginal plateaux and rift troughs: the Eastern, Queensland, and Marion Plateaux; the Pandora and Bligh Troughs; the Osprey Embayment; and the Queensland and Townsville Troughs and the Cato Trough. In addition, a zone of narrow rift basins extend southeast beneath the shelf of the GBR from the Queensland Trough southeast toward the Capricorn Basin and separating the Marion Plateau from the inner and middle continental shelf. The entire margin is underlain by modified continental crust formed as a result of fragmentation of a northeastern extension of the Tasman Fold Belt (Gardner, 1970; Ewing et al., 1970; Falvey, 1972; Falvey and Taylor, 1974; Taylor, 1975; Mutter, 1977; Taylor and Falvey, 1977; Mutter and Karner, 1980; Symonds, 1983; Symonds Davies and Parisi, 1984). The main physical and structural elements of offshore Queensland are shown in [Figure 1b](#) and briefly described below:

## Eastern Fields Plateau

The Eastern Plateau is the most northern marginal plateau of the northeast Australian continental margin ([Figures 1a, b](#), and [2a](#)) and is bounded in the west by the Moresby, Pandora, and Bligh Troughs, in the south by the Osprey Embayment, in the north by the Moresby Canyon, and in

the east by the Coral Sea Basin (Figure 1a and b). The plateau has an average depth of 1,500 m, and covers an area of about 31,000 km<sup>2</sup> at the 2,000 m isobath. Eastern Fields Reef, the only modern reef on the Eastern Plateau, is about 45 km across at its widest point, and lies at the crest of the plateau near its northern margin. Submerged and buried reefs extend northeast from Eastern Fields Reef beneath the Moresby Trough (Davies et al., 1988). The northern and southern plateau margins are controlled by normal faults; the western margin is more complex, and appears to be a product of thrusting. The Eastern Plateau is founded on a complex of tilt blocks bounded by reactivated normal faults, some of which appear to have undergone both wrench and reverse movement (Davies et al., 1988). This deformation appears to have resulted from Late Oligocene and Miocene tectonism caused by the development of the New Guinea Orogen to the north (Pigram and Davies, 1987). This late phase of structuring is not represented on the other northeast Australian marginal plateaux.

### Queensland Plateau

The Queensland Plateau is the largest marginal plateau on the Australian continental margin and is one of the largest features of its type in the world (Figure 1a and b). It is bounded on the northeast by the Coral Sea Basin, on the west by the Queensland Trough, and on the south by the Townsville Trough. The plateau is roughly triangular in shape, and extends over an area of about 165,000 km<sup>2</sup>. Approximately half of the plateau surface lies above the 1,000 m isobath, with living reef systems at or near present sea level making up 10–15% of the surface. The largest modern reef complexes are Tregrosse and Lihou Reefs, lying along the southern margin of the plateau (Figure 1a). Both these complexes are nearly 100 km long from east to west, and 50 and 25 km wide, respectively, from north to south. The other major areas of modern reef growth are the Coringa, Willis, and Diana complexes, which are aligned north to south in the center of the plateau, and the large isolated pinnacles of Flinders, Holmes, Bougainville, and Osprey Reefs, which lie along the western margin of the plateau (Figure 1). In addition, drowned reefs have been reported from at least 25 different locations (Taylor, 1977; Mutter, 1977; Davies et al., 1988). Away from reef areas, the plateau surface is generally smooth and slopes northward. A distinct terrace at approximately 450–500 m depth connects both the Willis and Diana reef complexes and the Tregrosse-Lihou-Coringa reef complexes.

### Marion Plateau

The 77,000 km<sup>2</sup> area of the Marion Plateau lies directly east of the central Great Barrier Reef, and is bounded along its northern margin by the Townsville Trough and along its eastern margin by the Cato Trough (Figure 1a). The present plateau surface forms a deep water extension of the shelf of the central Great Barrier Reef, with water

depths ranging from 100 m along the western border to 500 m along the eastern margin. At present, reef growth is restricted to Marion Reef, on the northeastern corner, and Saumarez Reef, at the southeastern corner of the plateau (Figure 1a).

The Marion Plateau is bounded on three sides by rifts: the Cato Trough to the east, the Townsville Trough to the north, and in the west by a series of north–south-oriented, narrow half-grabens which separate the plateau from the Australian continent (Figure 1b). The most northern of these half-grabens appear to join the confluence of the Townsville and Queensland Troughs. In the early Tertiary, therefore, the Marion Plateau formed a separate marginal plateau. The basement beneath the Marion Plateau is a planated surface dipping gently northeast (Figure 2d and e). The only disruption to this surface occurs in the northeast corner where a basement high forms the pedestal on which Marion Reef developed. Basement beneath the plateau margins is steeply down-faulted into the troughs to the north and east and was completely transgressed during the Early Miocene, resulting in the development of an extensive carbonate platform on which four, progressively more, restricted reef growth phases occurred, the last of which is seen today on Marion and Saumarez reefs. Over most of the platform, shallow water carbonates ceased with late upper Miocene/Pliocene subsidence.

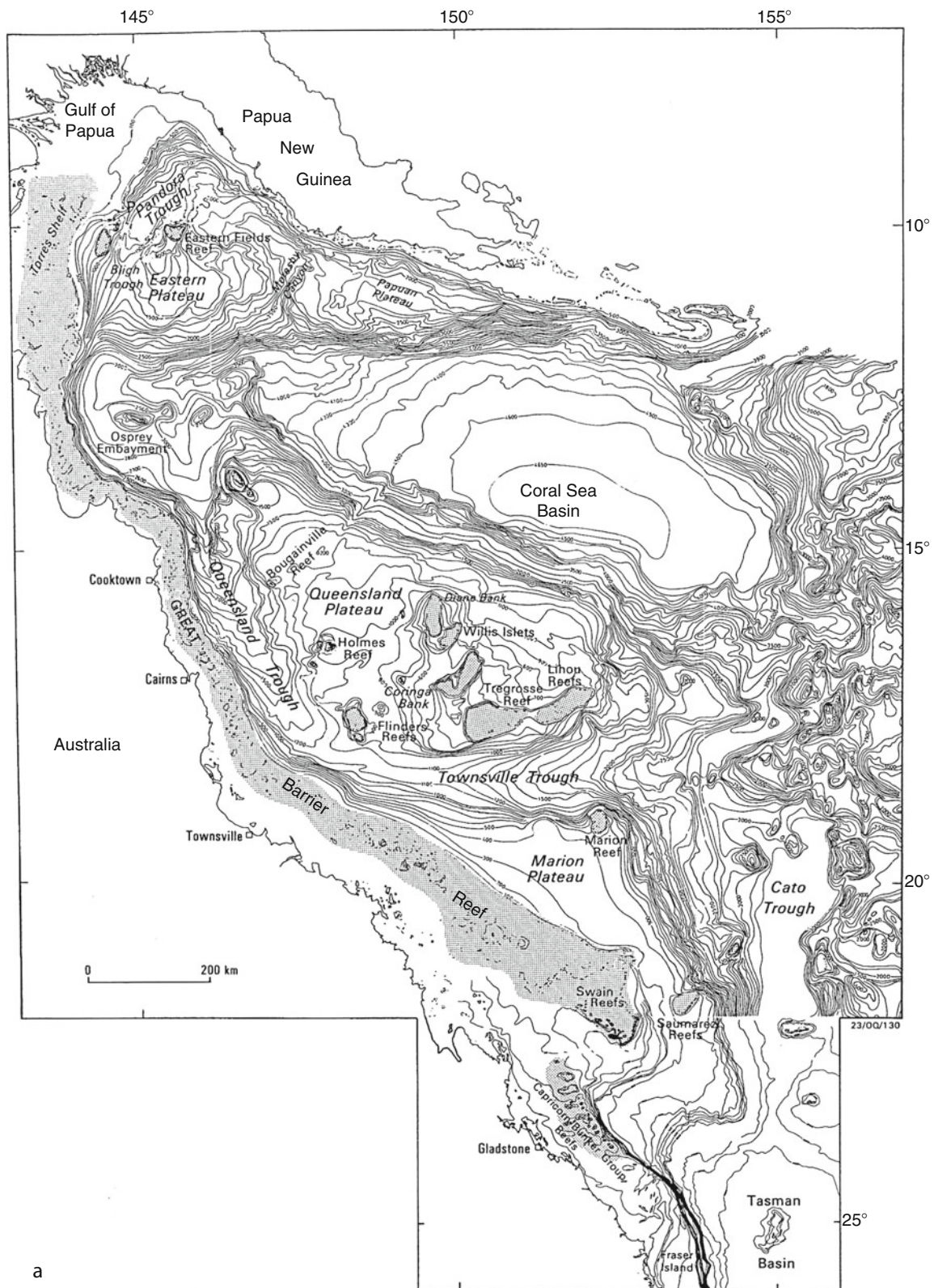
### The Swains Reef and Bunker Highs

The Swains Reef high (Figure 1a and b) is a structural high some 200 km long and 50 km wide to the southwest of the Marion Plateau and forming the eastern boundary of the Capricorn Rift basin (Figure 1b). It is probably a late Cretaceous feature when it formed the eastern side of the Maryborough basin, but became a prominent late Tertiary feature when rifting jumped from the Maryborough to the Capricorn basin and sea floor spreading unzipped northwest in the Cato Trough. Marine conditions were established over the Swains High probably in the late Oligocene/early Miocene. It is thought that reefs established in the Pleistocene. The Bunker High occurs to the southwest of the Capricorn Basin (Figure 1a and b). It formed an eastern volcanic source for the Cretaceous Maryborough Basin and following rifting in the Tasman Sea, the western edge of the Cainozoic Capricorn Basin. It was transgressed in the Miocene with shallow water marine calcarenites and foraminiferal limestones establishing as precursors to reefs in the Pleistocene of this southern region.

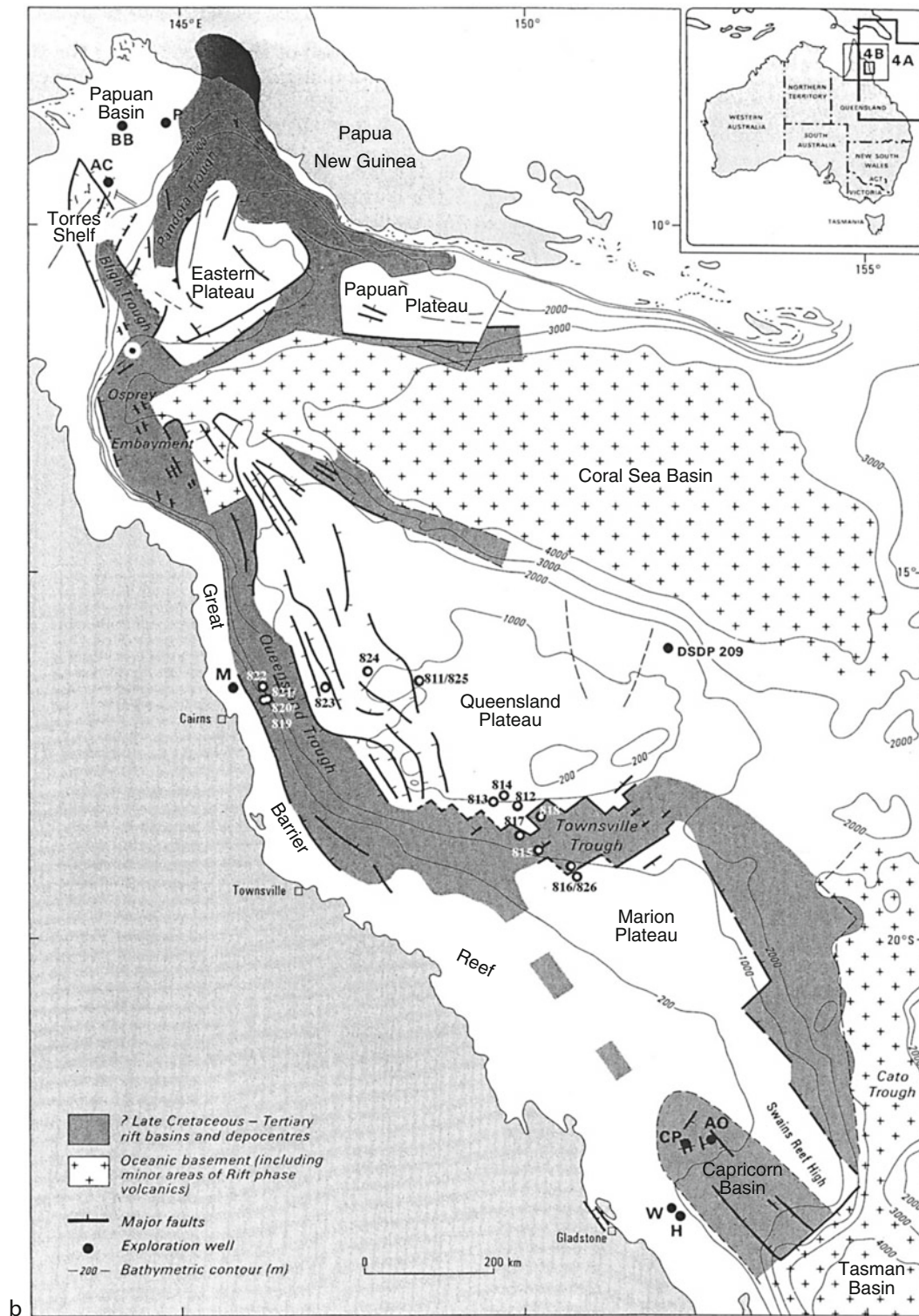
### The Great Barrier Reef

The Great Barrier Reef is a modern reef system which extends along the northeast Australian margin from 24.30 to 9.30°S (15° of latitude), a distance of 2,300 km from north of Fraser Island in the south to the Torres Shelf/Gulf of Papua in the north. There are estimated to be in excess of 3,600 individual reefs within this area.



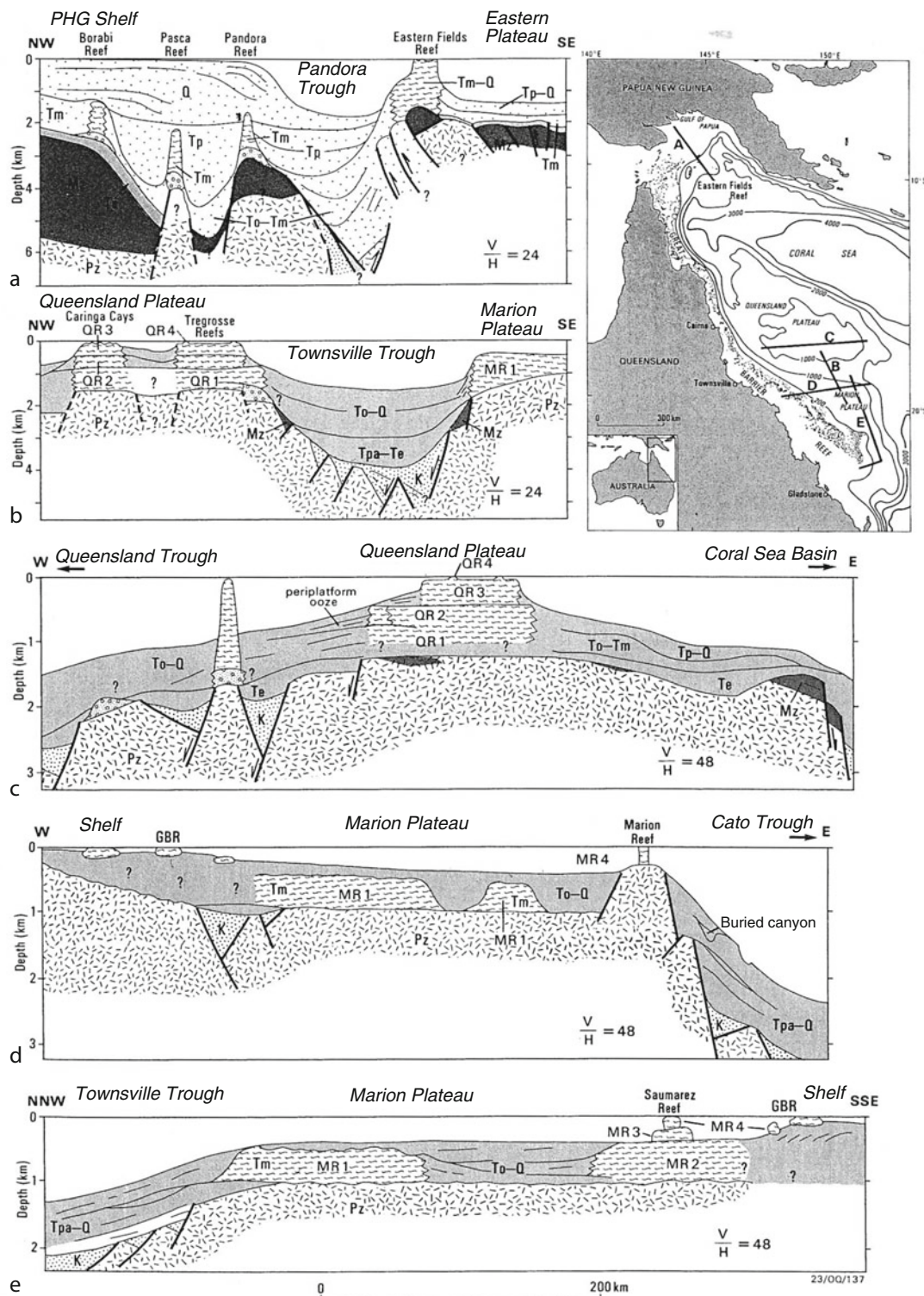


Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 1 (Continued)



**Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 1** (a) The main physical features of the northeast Australian margin showing in particular the Great Barrier Reef, together with the other main plateaux and rifts. (b) The major structural features of northeast Australia. The location of major drill holes are shown (BB Borabi, P Pasca, AC Anchor cay, M Michaelmas cay, AQ Aquarius, CP Capricorn, W Wreck, H Heron, 209 DSDP 209, 811–824 ODP sites).



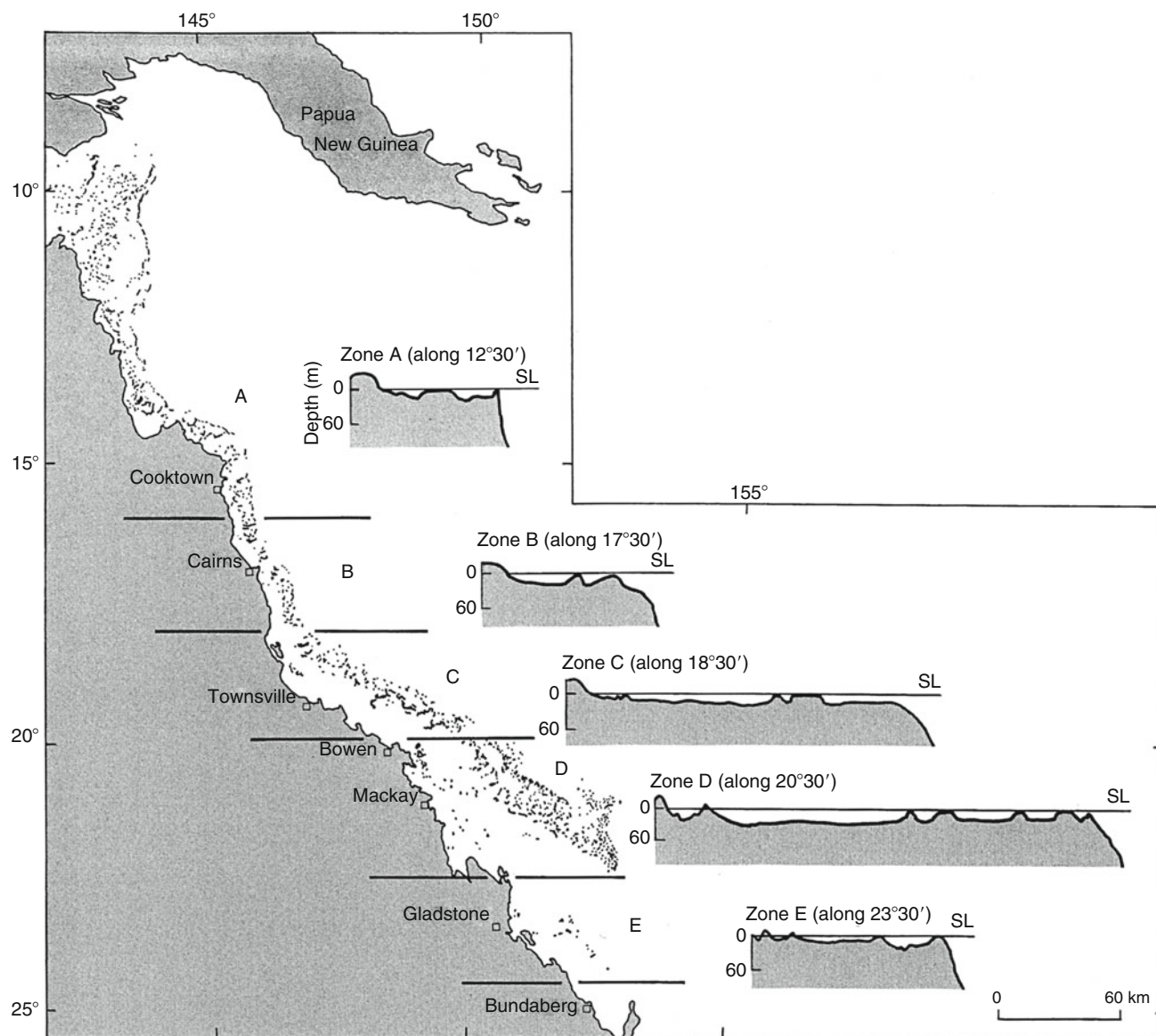


**Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 2** Schematic sections showing the generalized structure and sedimentary relationships on (a) the Eastern Fields Plateau, (b) north to south through the Queensland Plateau (c), west to east through the Queensland Plateau (d) east to west through the Marion Plateau and (e) north to south through the Marion Plateau.



The shelf occupied by the Great Barrier Reef is narrowest in the north along 14°S (23 km) and widest in the south along 21°S (260 km) (Figure 3). Reefs occupy the whole shelf in the northern region, but apart from fringing reefs along coasts and large islands, reefs occur largely in the mid- to outer shelf in the center and south. The bathymetry is complex and varies regionally, but six distinct bathymetric regions can be defined (Figures 1 and 3). Area A (Figure 3) in the extreme north (9–12°S) is a narrow rimmed high-energy platform characterized by a shallow narrow shelf (50–75 km wide) and a steep continental slope. Reefs occur in four clearly delineated groups: the reefs of the western Torres Shelf, the Warrior

line continuing northward off the end of Cape York, the mid-shelf plethora of small patches, and the outer shelf barrier reefs. In the region 12° and 16°S the shelf is no more than 50 km wide except east of Cape Flattery where it achieves 75 km. Water depths are generally shallow, the outer shelf being the only place where water depths greater than 50 m occur. The most prominent reef features in the region are the outer shelf line of barrier or ribbon reefs forming an almost continuous shelf edge between Capes Grenville and Flattery but still prominent down to about latitude 17°S and east of which the continental slope is precipitous to a depth of 200–300 m, and also the gigantic mid-shelf platform reefs, particularly, northeast of



Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 3 Physiographic variation in the Great Barrier Reef province.

Princess Charlotte Bay. Area B (Figure 3) occurs between Cape Bedford and Hinchinbrook Island (16° and 18°S), where the shelf varies in width from 50 to 75 km, and is bathymetrically relatively simple. Reefs generally occur as fringing reefs along the coast and as large platform and ribbon reefs on the mid- to outer shelf; these are separated from the coast by a channel or inner lagoon with water depths of around 35 m. The outer shelf ribbon reefs form a discontinuous barrier particularly in the northern part of the area but becomes gradually more discontinuous to the south, ceasing to exist as a line of reefs to the south of Cairns, at latitude 18S but continuing as line shoals on the shelf edge averaging 60 m water depth. Area C (Figure 3) occurs between Hinchinbrook Island and the Whitsunday Islands (18° and 20°S) where the shelf takes a clear change in direction, changing from north–south to north–west to south–east. The width of the shelf also widens considerably to an average of 90–125 km. The inner 50–80 km of the shelf is reefless except for fringing reefs attached to high islands but eastward, the mid- to outer shelf slopes gently from 45 to 75 m, at which depth a marked change in slope occurs, reflecting the inner edge of an outer shelf terrace some 20–30 km in width. The Slashers, John Brewer, Myrmidon, Pith, Wheeler, Keeper, Bowl, Stanley, and Viper reefs occupy this outer shelf terrace. A drowned barrier reef complex occupies the outer shelf of the 75 m terrace and extends to the south-east for 200 km. Area D (Figure 3) occurs between the Whitsunday Islands to the Swain Reefs (20° to 22°S), the shelf continuing its northwest to southeast orientation away from the coast giving rise to a dramatic increase in the width of the shelf to over 300 km in the south. The inner two thirds of the shelf are reefless except for small fringing reefs around continental islands; eastward, however, the outer shelf is a plethora of gigantic reefs forming the Pompey complex and smaller more dispersed reefs forming the Swains complex. Area E (Figure 3) occurs to the south of the Capricorn Channel (22° and 24°S) where the shelf is less than 100 km wide, with the Capricorn and Bunker reefs occupying only a narrow zone on the mid-shelf. Well-known reefs in the region include Heron, Wreck, One Tree, Fitzroy, Fairfax, and Lady Musgrave.

Small drowned reefs occupy the shelf edge in 80–100 m of water (Davies et al., 2004). In addition to the reef ecosystem, *Halimeda* bioherms and biostromes comprise an almost equally important ecosystem in the northern and central, southern Great Barrier Reef (See *Halimeda Bioherms*, this volume).

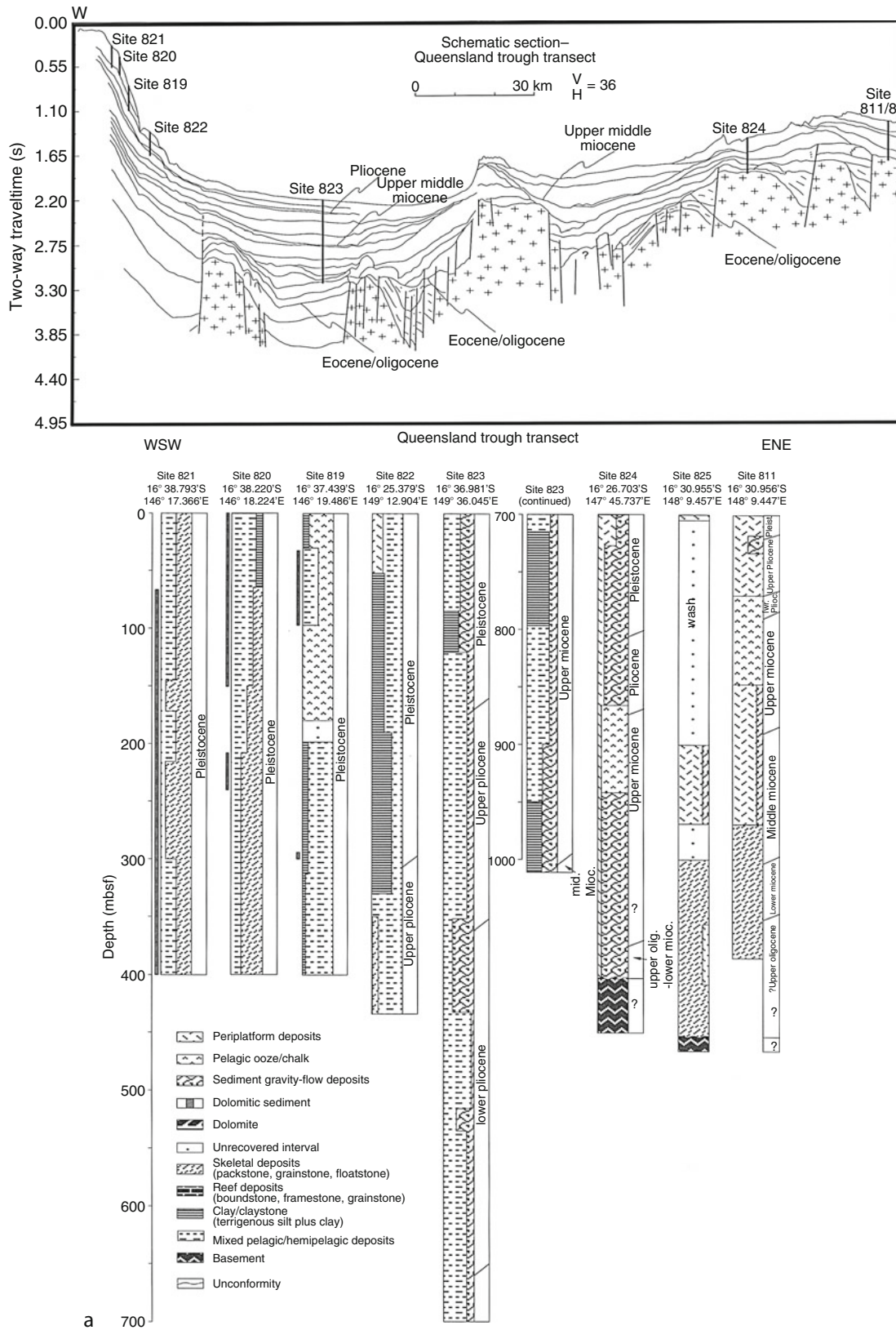
### The rift basins

In addition to the platforms, the architecture of the north-east Australian margin is dominated by a series of rift basins (Figure 1a and b) which formed as a result of fragmentation of a northeastern extension of the Tasman fold belt (Gardner, 1979; Ewing et al., 1970; Falvey, 1972; Falvey and Taylor, 1974; Taylor, 1975; Mutter, 1977;

Taylor and Falvey, 1977; Mutter and Karner, 1980). The Pandora and Bligh Troughs and the Osprey Embayment occur in the north; the Queensland and Townsville Troughs in the central region and the Cato trough occupies the eastern and southern sections of the GBR. Relatively, smaller rift basins are also known to underlie the shelf of the Great Barrier Reef – the Papuan platform, the Halifax basin, the Whitsunday basin, and the Capricorn basin (Figure 1a and b). In the north the Papuan platform is a thick (? 4–5 km) Jurassic to Recent basin containing reefs within a fluvio-deltaic sequence representing the vast outpourings from the Fly River in New Guinea. The poorly defined Halifax Basin is a major structure beneath the continental shelf to the east of Townsville and underlies the central outer GBR: it is a Cretaceous/Tertiary basin covering some 60,000 km<sup>2</sup> and a maximum thickness in excess of 4,000 m. It lies at the intersection of the Queensland and Townsville Troughs. The Whitsunday Basin is a very shallow structure containing little more than 1,000–1,500 m of Cretaceous/Tertiary sediments underlying the region to the west of the Pompey and Swains reefs and may represent a connection between the Halifax and Capricorn basins. In the south, the Capricorn basin is sandwiched between the Bunker and Swains Highs.

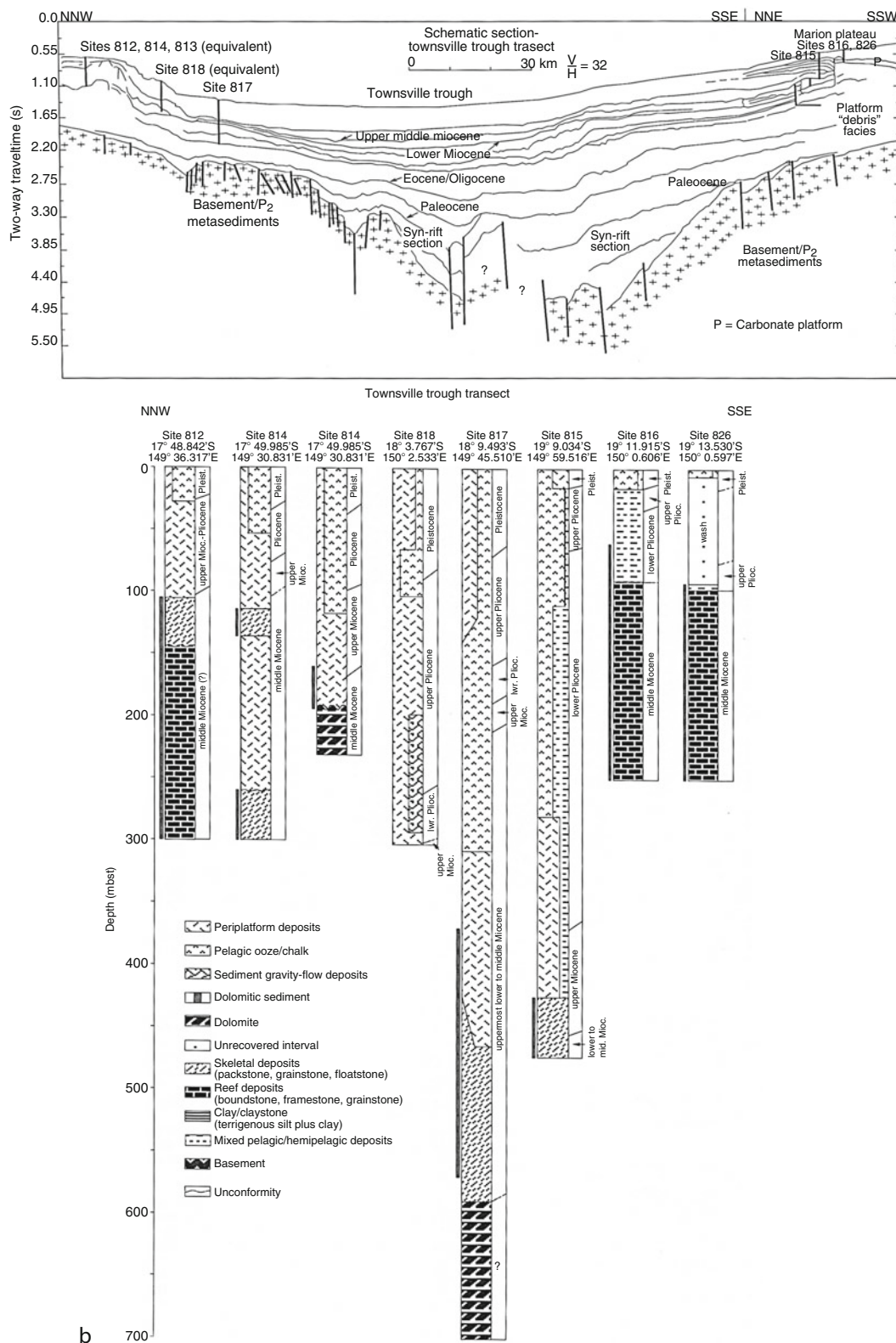
### Bunker and Swains Highs

The Queensland and Townsville Troughs lie adjacent to the central/ northern reef region. Directly adjacent to the Great Barrier Reef (Figures 1a, b and 4a, b), the Queensland Trough occupies the region between the continental shelf and the Queensland Plateau between 14°S and 17°30'S. The floor of the trough slopes northward from 1,000 m at the junction with the Townsville Trough to around 3,000 m at its junction with the Osprey Embayment. Rather than being a simple graben, the Queensland trough may have been initiated in an oblique wrench zone caused by left-lateral movements between Australia and the Queensland Plateau (Symonds et al., 1984). The Townsville Trough is a west to east trough separating the Queensland and Marion Plateaux. It is over 500 km in length and 150 km wide. At its confluence with the Queensland Trough, the Townsville Trough is 1,000 m deep, deepening eastward to 3,000 m at its exit into the Coral Sea Basin. At this eastern end, at about Longitude 154°E, a bifurcation sends one branch south into the Cato Trough and the other winding sinuously north into the Coral Sea Basin. The Capricorn Basin started in the late Cretaceous as the result of an eastward shift of the Maryborough basin rift axis to the east concomitant with spreading in the Cato Trough. The basin extends in a northwest to southeast direction and is 500 km long by 250 km wide and is bordered by the Bunker and Swains Highs. This early to late Cretaceous rift phase development preceded continental breakup and the formation of the Coral Sea Basin by sea floor spreading in the Paleocene (62–56 million year BP) or latest Cretaceous (Weissel and Watts, 1979; Symonds et al., 1984).



Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 4 (Continued)





**Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 4** (a) Cross section of the Queensland trough and the stratigraphy of ODP drill holes across the trough; (b) Cross section of the Townsville trough and stratigraphy of ODP drill holes across the trough.

A major outcome was the development of a series of interconnected three-branch rift systems with the Townsville and Queensland Troughs and the Osprey Embayment representing failed arms of such a system (Mutter and Karner, 1980). These troughs are the most important structural elements associated with the formation of the Great Barrier Reef Province.

### Causes of architecture

The causes of the architecture described above are rifting, drifting, subsidence, sea-level/climate change, and collision. These are briefly summarized as follows:

#### Rifting

Late Cretaceous extension formed the basins described above, all of which are rift basins proximal to carbonate platforms. Of particular importance is the Queensland-Townsville-Cato rift systems, but also of importance if less developed is the rift system extending south from the Queensland trough through the Whitsunday basin to the Capricorn basin separating the Queensland shelf from the Marion and Queensland plateaux. The rifting process has clearly influenced the form of platform development in both, a general way through influencing the shape of the platforms and providing a substrate for shallow water deposition, but also in a specific way through the influence of fault blocks as sites for early reef development (Figures 2 and 5a, b).

#### Subsidence

The effect of subsidence is mainly to produce space. It can also have the effect of termination. Quantitative subsidence data for northeast Australia in four wells, Anchor Cay 1, DSDP Site 209, Capricorn 1A, and Aquarius 1 are shown in Figure 6. This data indicates that northeast Australia has not subsided solely as a result of uniform post-rift thermal cooling; rapid subsidence pulses have occurred at different times, and such pulses have clearly initiated transgressions. In the northern region at Anchor Cay, subsidence increased to 50 m/million years in the Miocene and increased again to 149 m/million years in the Pliocene. On the Queensland Plateau, at ODP site 209 subsidences doubled after the middle Miocene. In the Capricorn Basin, major subsidence of 75 m/million years occurred in the middle Oligocene and again in the Pliocene with uplift in the intervening early Pliocene. In the north and south, subsidence pulses occurred in the Miocene and the Pliocene. Seismic data from the central to northern shelf (Townsville to north of Cairns) shows a mid-shelf hinge of subsidence, delineating the point from which sediment packages thicken eastward. The northern shelf north of Cairns lies dominantly west of this hinge line; in the central region, most reef development occurs adjacent to the hinge line whereas southwards the Pompey and Swain reefs occur well to the east of the hinge line. There is fundamental control of reef growth by basement subsidence.

#### Drift

Hotspot (Duncan, 1981; Wellman, 1983) and magnetotratigraphic studies (Idnurm, 1985, 1986) define the basis for reconstruction of Indian-Australian plate motion through the Cenozoic (Figure 7a). Since the late Eocene when northeast Australia was located between 29° and 44°S, the continent has moved almost directly northward to its present position between 9° and 24°S. This movement would have resulted in profound climatic changes along the northeast Australian margin. Simplistically (Figure 7), the northern tip of northeast Australia would have entered the tropics only 25 Ma ago whilst the southern part of the Great Barrier Reef would have entered the tropics only in the last 1 Ma with substantial impact on the likely sedimentary facies that could have formed. However, a more detailed analysis of the effects of plate motions on paleo-oceanography (see Davies et al., 1989, p. 65) gives a much more precise analysis (Figure 7b) from which the following conclusions are drawn:

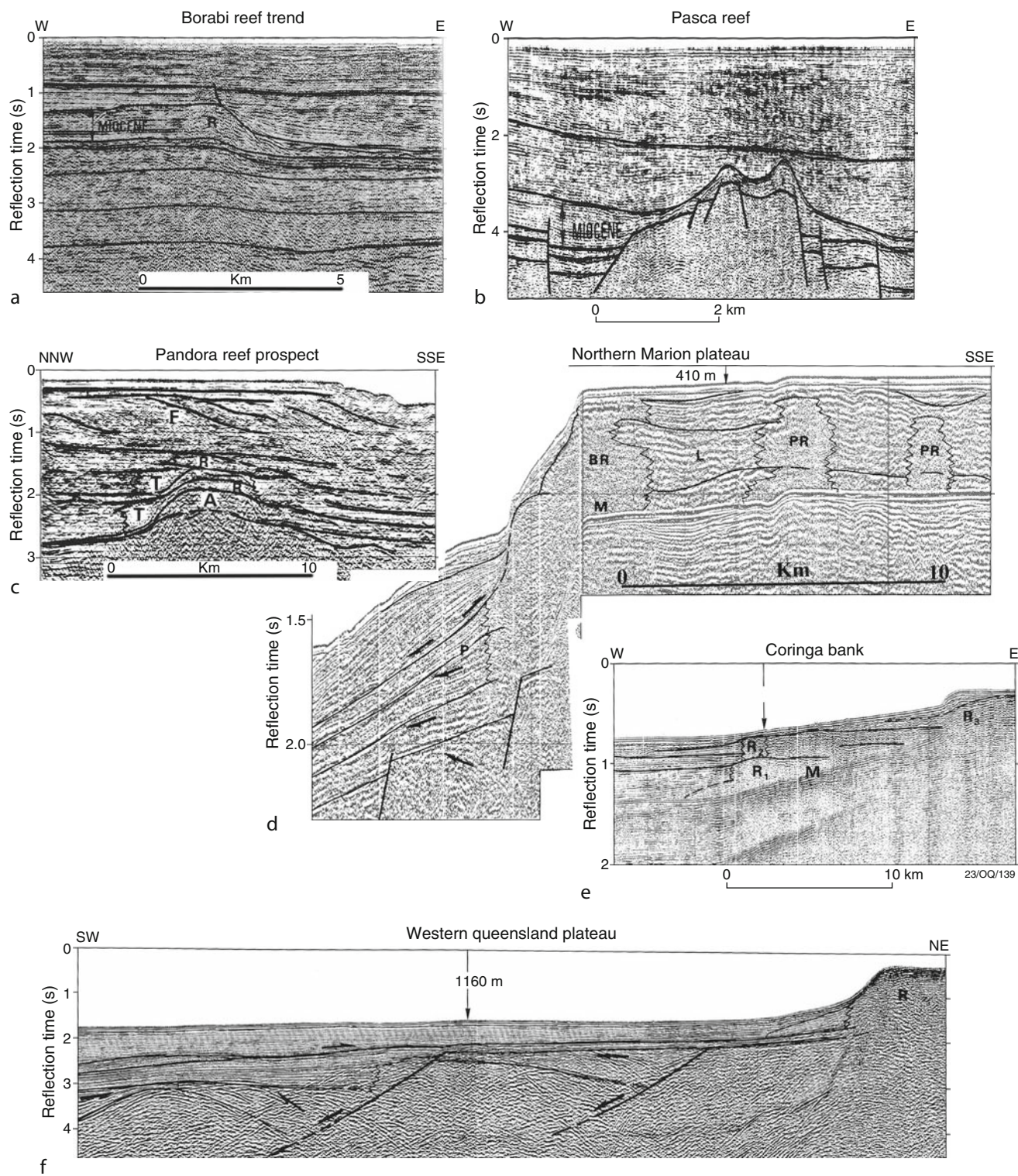
1. In the earliest Eocene, temperatures were very briefly warm enough for coral reef growth. Chaproniere (1984) reported large foraminifera from a dredge haul off the northwest Queensland Plateau, which he concluded grew in waters with temperatures of 18–27°C.
2. Sea surface temperatures from the middle Eocene to the middle Early Miocene (44–19 Ma) over the whole northeast Australian margin were temperate.
3. During the early Miocene sea surface temperatures off northeast Australia were marginal for coral reef development. In modern parlance, they were subtropical, comparable to southern Queensland today.
4. A rapid rise in sea surface temperatures occurred in the early mid-Miocene. Conditions were warm enough for coral reef growth in the northern and central GBR.
5. During the upper Miocene, tropical conditions persisted in the north and center but warming slowed in the south and conditions were not conducive for coral reef growth. Subtropical conditions prevailed in the south.
6. During the Pliocene and Pleistocene, the entire northeast Australian margin was situated within the tropics.

The consequences of these apparently simple conclusions are substantial and fundamental for northeast Australia:

- a. Any tropical platform must be underlain by a temperate platform and that initial rifting of the margin will contain temperate facies sediments.
- b. The consequence of the drifting model of sediment development is that reefs grew first in the north and, progressively, later in the south depending on SST.
- c. Tropical facies development will thin southward and overlie a progressively southerly thickening subtropical to temperate section. Facies diachroneity is, therefore, a fundamental factor of a stratigraphy dominated by plate motion through climatic belts.

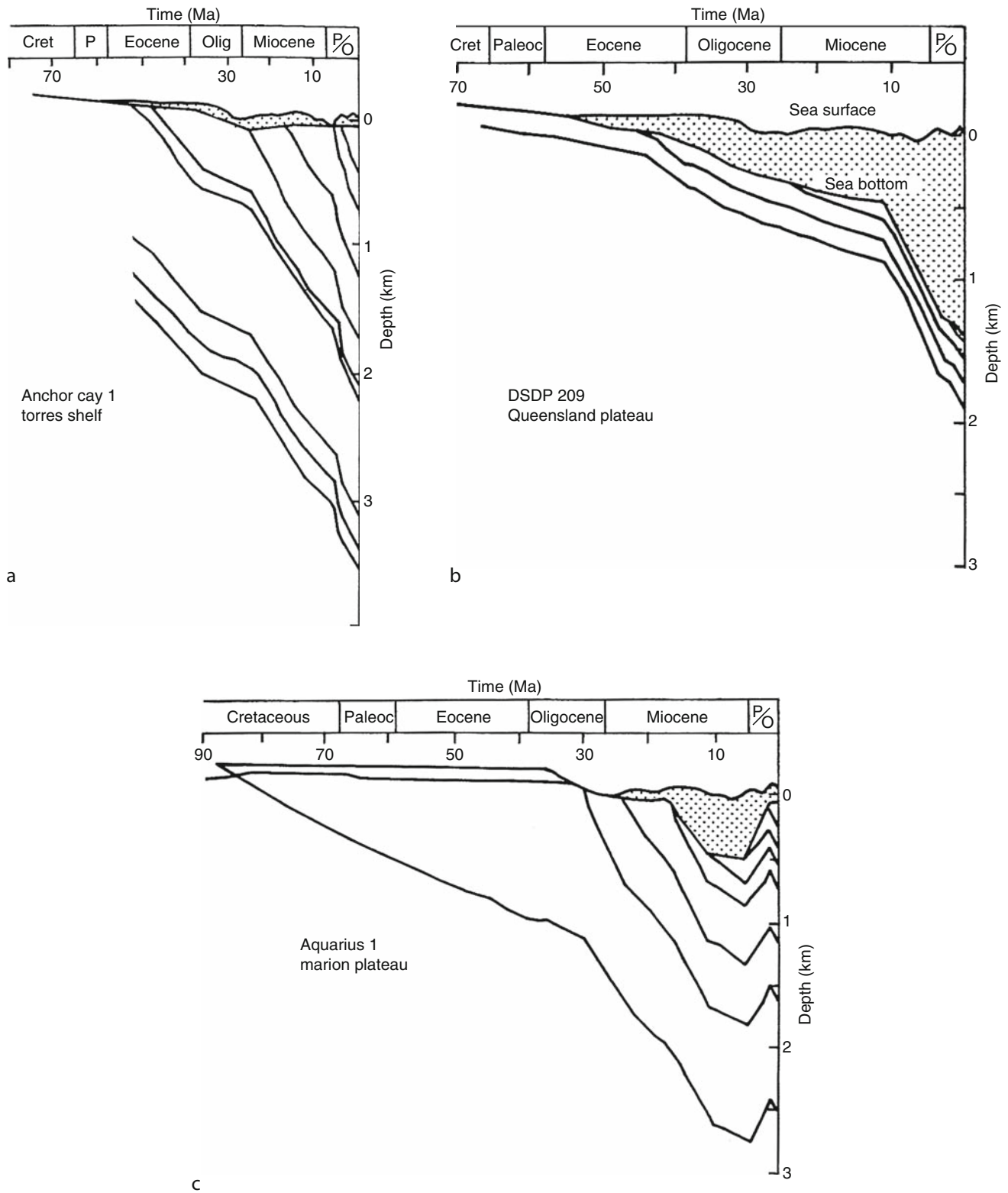
The conclusions can be tested by comparing present day facies distributions along the east Australian margin with



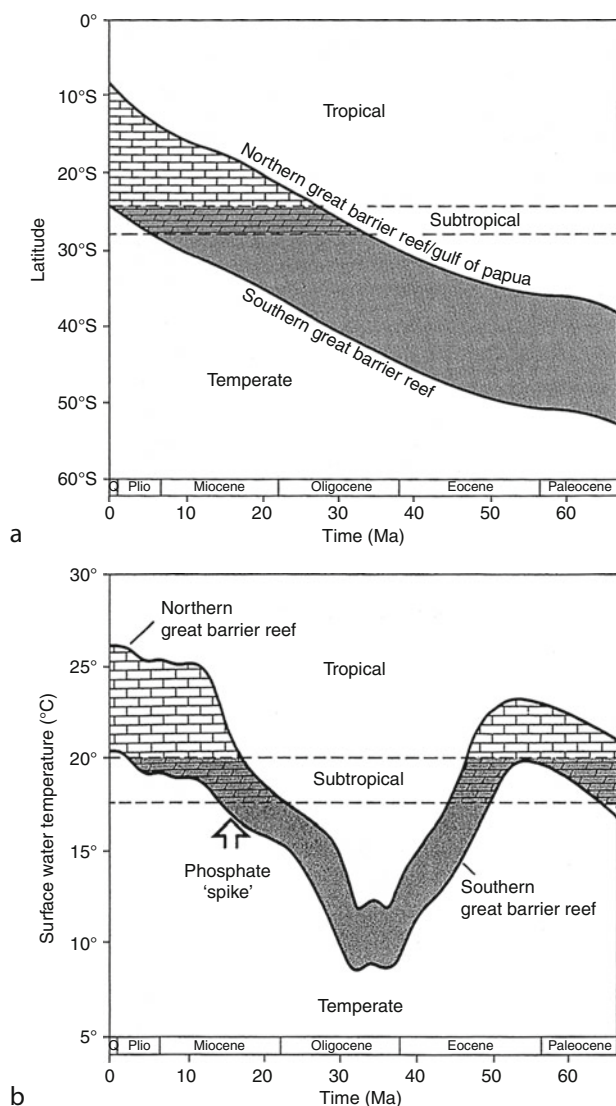


**Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 5** Seismic sections across (a) Borabi, Pasca, Eastern Fields Plateau and Pandora Trough and (b) northern margin of the Marion Plateau showing the plateau edge reefs. Both sections show the importance of faulted margins as the sites for large reef systems. (c) western parts of the Queensland Plateau.





**Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 6** Subsidence history for drill holes at Anchor cay, DSDP Site 209, Aquarius and Anchor Cay.



### Great Barrier Reef: Origin, Evolution, and Modern

**Development, Figure 7** (a) Projected latitudinal movement of northeast Australia throughout the Cenozoic. The northern boundary corresponds to Anchor Cay (presently 9°30'S) and the southern boundary to Heron Island (presently 24°S). (b) Surface water temperature envelope for the northeast Australian region throughout the Cenozoic, showing periods when temperatures were suitable for reef growth. The Miocene "phosphate" spike which inhibited reef growth is also shown (see Riggs, 1984).

the vertical facies seen in drill core from the Gulf of Papua. The present day sediment distribution on the outer continental shelf shows three major facies (Marshall and Davies, 1978):

North of Latitude 24S-tropical carbonate and clastic sediments dominated by corals and *Halimeda*.

Latitude 24–28S – subtropical coralline algal coated grains (rhodoliths), encrusting foraminifera, bryozoa.

South of latitude 28S – branching bryozoan/foram/molluscan facies.

A similar facies sequence occurs vertically in the Borabi No. 1 drill hole in the Gulf of Papua (Figure 8a). The bottom to top facies variations mirror those on the present shelf from south to north, and including the change to foreland basin clastics in the Gulf of Papua. The effects of drift, therefore, are as shown in Figure 9.

### Sea-level variations

Operating relatively in conjunction with subsidence, the effects of sea-level variations on platform development on the northeast Australian margin are different on the continental shelf and the marginal plateaux. On the shelf, high sea levels are carbonate-dominated and low sea levels are terrigenous-dominated on shelf and slope, and unconformities are widespread. However, on the oceanic plateaux where no terrigenous source occurs, high stands are reef or periplatform dominated and lowstands are dominated by unconformity development and caliche formation on the platform and carbonate gravity deposition and peri-platform deposition on the steep slopes.

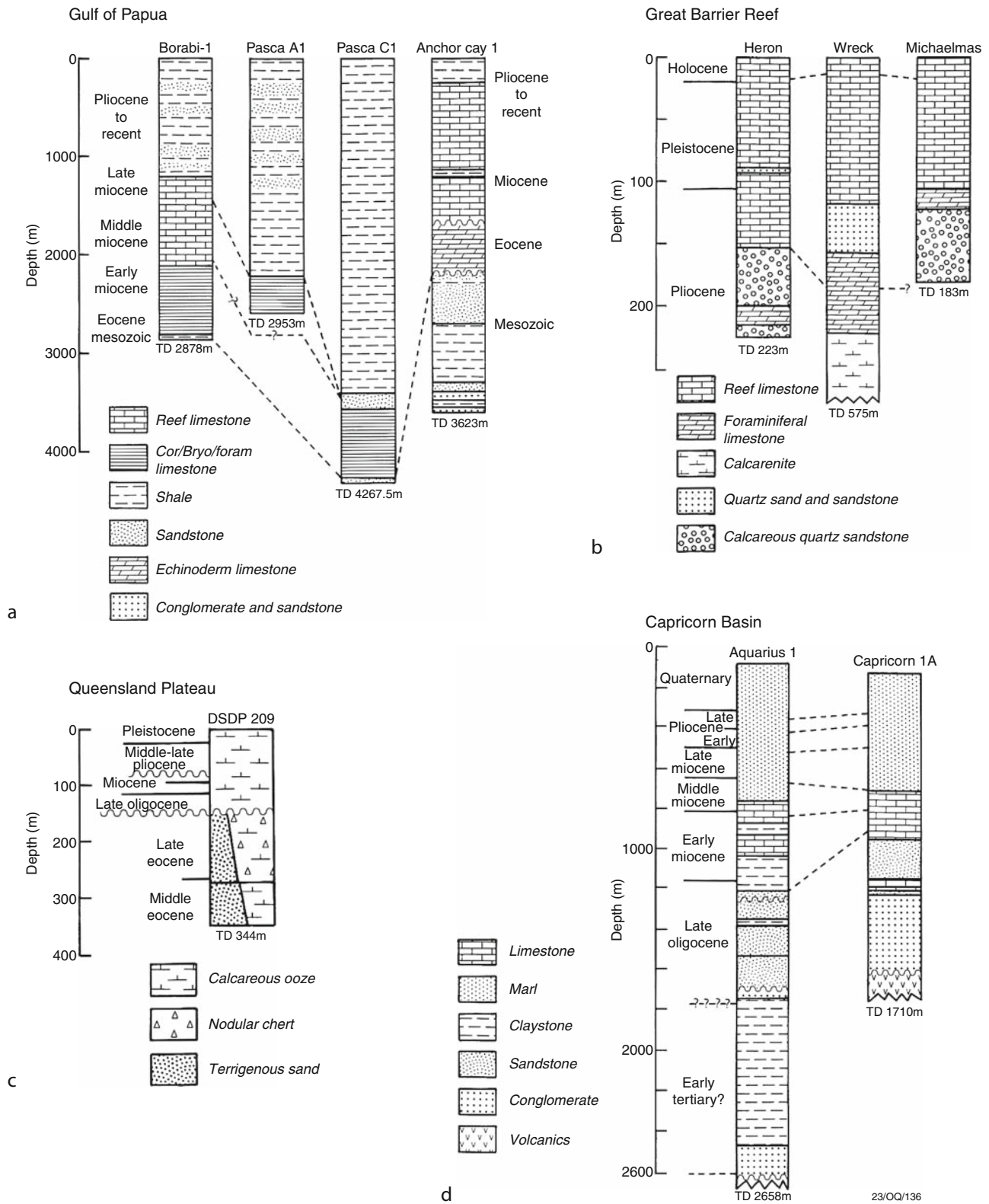
### Collision

If, as a result of plate motion, a passive margin moves into a compressional tectonic regime, the carbonate platforms developed on that margin will be profoundly affected. They will become embroiled in mountain building and possibly subduction. These effects are seen on the northern edge of the Australian craton, which collided with an island arc complex in the Oligocene. The sequential development of the platform during collision is shown in Figure 10. This convergent history, leading to foreland basin development and mountain building, paradoxically, first led to an expansion of the area of carbonate deposition, but was followed by contraction, demise, and burial of the carbonates by clastic detritus (Pigram and Davies, 1987; Davies et al., 1989). This may be the fate of the whole of the GBR if Australia's northern motion is not arrested.

### Establishment of reefs in northeast Australia

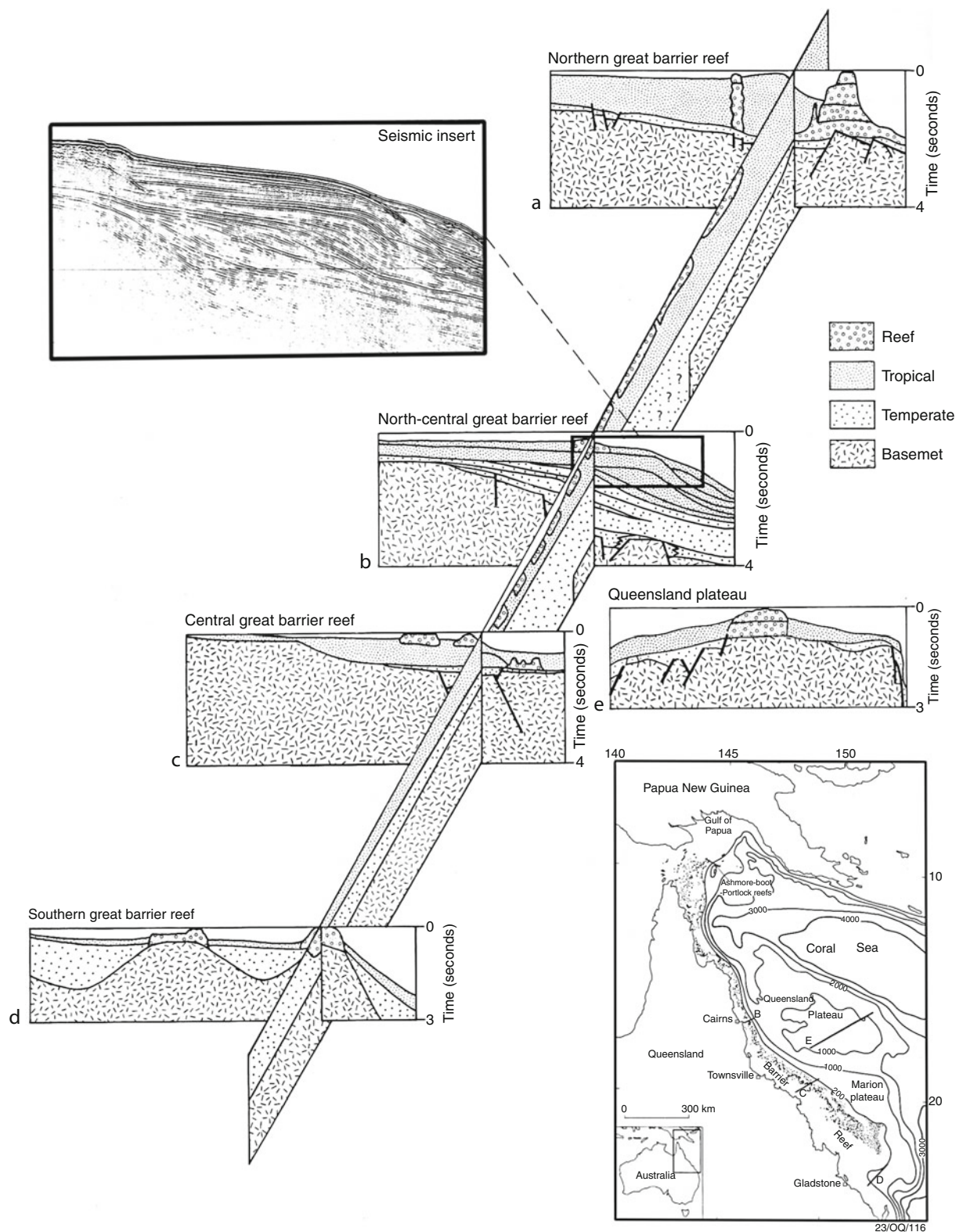
As a consequence of the processes and architecture described above, coral reefs have been established on three occasions (1) in the early to late mid-Miocene (2) in the uppermost Miocene, and (3) in the Pleistocene.

Reefs first established on the Papuan shelf at Borabi and Pasca. Seismic (Figure 5) and drill hole data (Figure 8) show early to mid-Miocene reefs at Borabi established on pre-reefal red algal banks and also on a basement high at Pasca. On the Queensland Plateau (Figures 4 and 5b) reefs established in the Middle Miocene, once again on red algal banks (Brachert et al., 1993). On the Marion Plateau (Pigram et al., 1992) an extensive reef system covered over 400 km of the plateau and was established and reestablished on the plateau and along its northern edge (Figures 4 and 5). These reef systems terminated at different times and for different reasons.



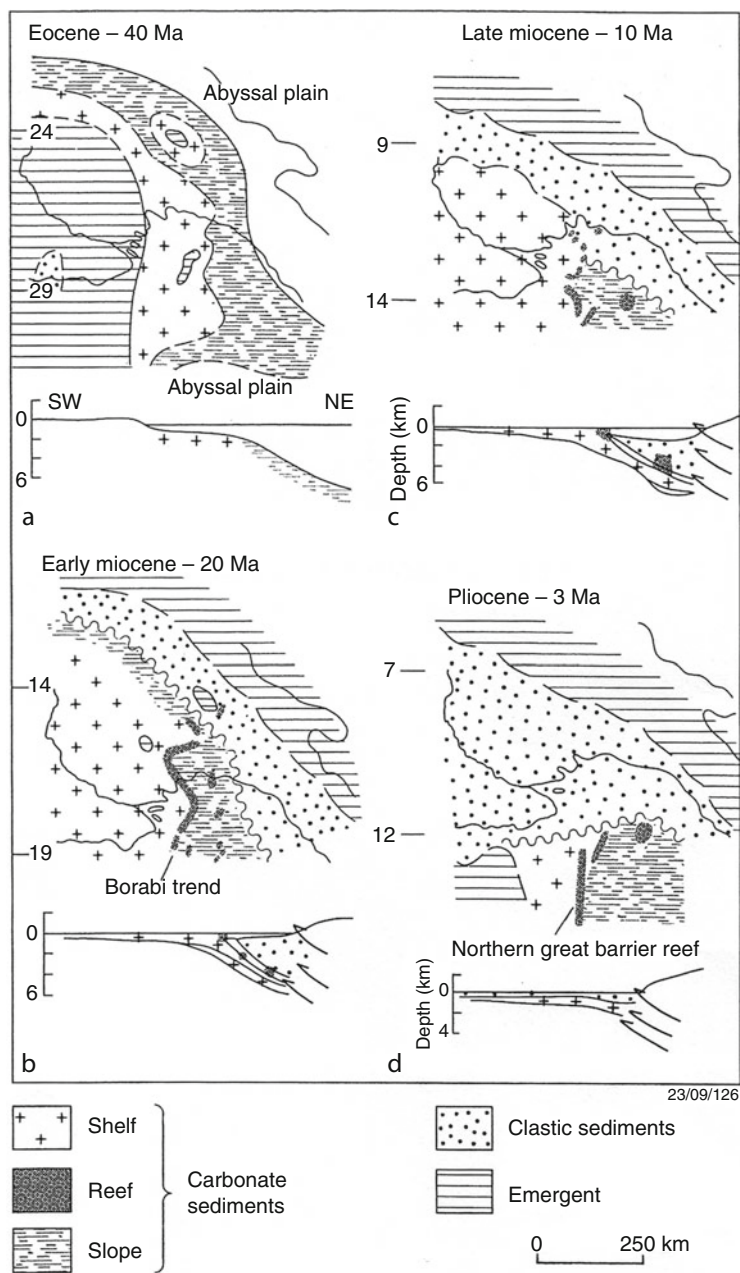
Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 8 Details of drill holes on the northeast Australian margin.





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**Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 9** Aspects of the structural history and sedimentologic framework of northeast Australia illustrated by schematic sections across the north, central and southern regions. An interpretative north to south tie shows the thinning and thickening of tropical and temperate sediments as a consequence of drift.



**Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 10** Cenozoic palaeo-oceanography of the Gulf of Papua/northern Great Barrier Reef showing the effects of progressive foreland basin development on carbonate platforms during (a) Eocene, (b) Early Miocene, (c) Late Miocene and (d) Pliocene. The schematic sections are orientated approximately northeast-southwest. Approximate palaeolatitudes are shown for each section.

In the north, reef growth at Borabi and Pasca through development of the foreland basin, and the southward flooding of fluvio-clastics caused the eventual migration of reefs eastward. On the Queensland Plateau, reefs terminated at 13.7 Ma due to subsidence of the plateau. On the Marion Plateau, reef growth terminated at 10.7 Ma as a consequence of a major fall in sea level in excess of a 150 m (Pigram et al., 1992).

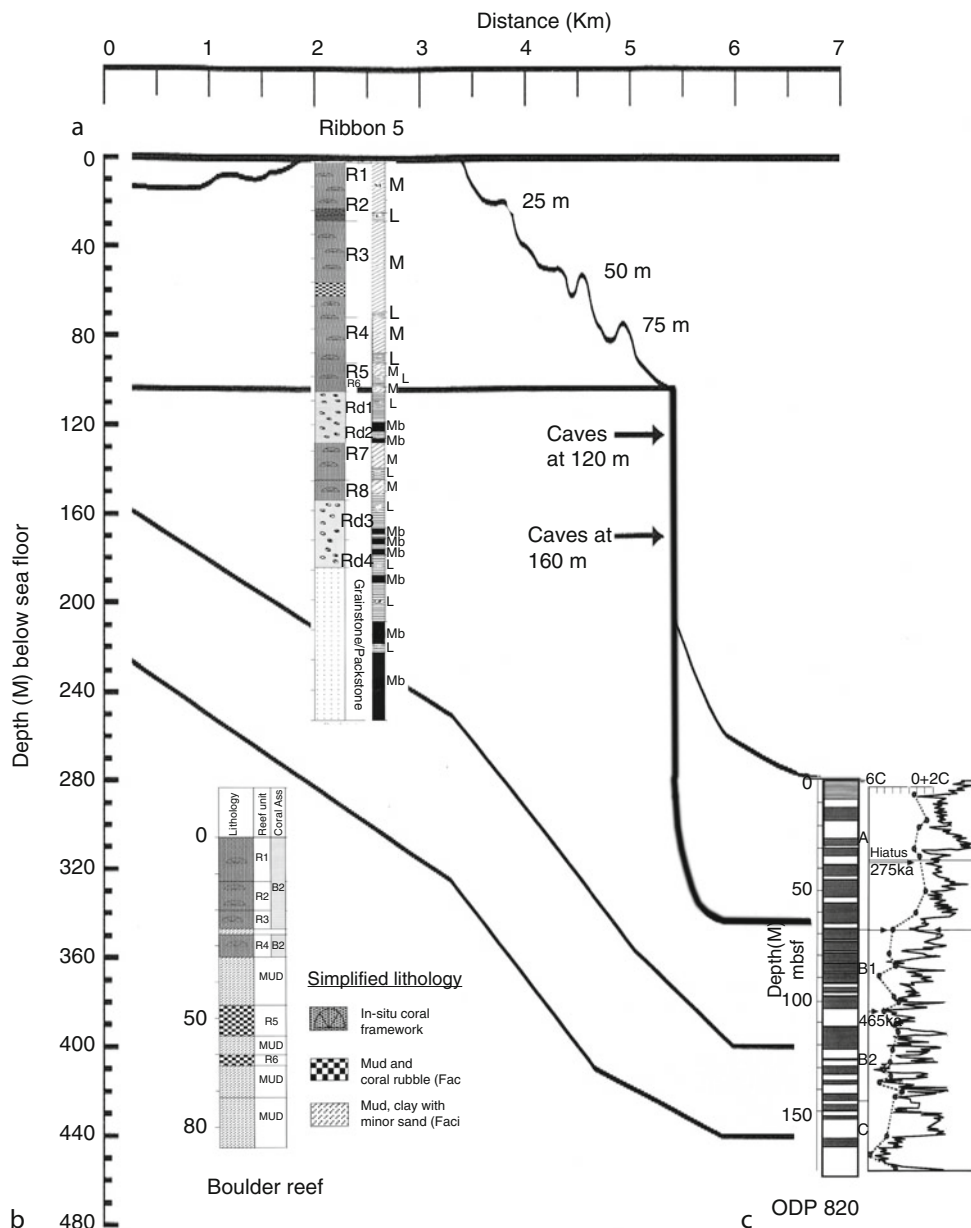
Reefs reestablished in the north on Anchor Cay and Pandora in the upper Miocene and Pliocene, but not on the Queensland and Marion Plateaux for two reasons. First, an upper Miocene (7 Ma) subsidence pulse affected both plateaux (Figure 4) and secondly, oceanographic cooling established over the region at 6 Ma (Isern et al., 1993) inhibiting reef establishment, probably related to the Messinian glacio-eustatic sea-level fall. Reefs never

again established on the Marion plateau except at two places, Marion reef on the extreme northeastern edge and Suarez reef in the extreme southeast. This likely occurred in the Pliocene as it did on the Queensland Plateau (Figure 5c). This phase of growth substantially contracted on the Queensland Plateau by a third phase of subsidence at 3.7 Ma, drowning much of the plateau and in the north probably initiating further eastern migration of the reefs at Pandora. This pulse probably also established the main shape of the Australian continental shelf. However, the third phase of reef growth – the Great

Barrier Reef – did not establish at this time; it occurred much later.

### Establishment of the Great Barrier Reef

The Great Barrier Reef, as we know it, started in the late Pleistocene, much later than had been previously thought, and very much later than when the main architecture of the shelf had been established. The evidence for this is in the drill holes from Ribbon 5 and ODP 820 (Figure 11a). These data are summarized as follows



**Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 11** Stratigraphy defined for (a) Ribbon Reef 5. Ribbon 5 data also shows the reef front morphology and its correlation with ODP 820 (b) Boulder Reef, and (c) ODP Site 820.



### Ribbon Reef No. 5

Drilled in 1995, the detailed description of the corals, sediments (Webster and Davies, 2003) and coralline algae (Braga and Aguirre, 1997) in a core from Ribbon Reef 5 define the basis for understanding the establishment of the Great Barrier Reef. The litho-logs (Figure 11a) divide into three parts:

**0–96 m** – Six reef horizons comprised of two coral assemblages (1) robust branching *Acropora* (*humilis*, *robusta*, *palifera*, *Stylophora* (*pistillata*) and *Pocillopora* (*verrucosa*, *damicornis*) with associated massive *Goniastrea* and *Platygyra* and (2) Massive *Porites* (*lutea*, *solida*) with associated encrusting *Porites* and *Montipora*. Boundaries between reef horizons are identified by combinations of prominent horizons of pale brown sediment containing areas of calcitized plant cells, radiometric dating, negative shifts in  $\delta^{18}O$  values, exposure horizons, color changes from pink to brown, changes in algal associations and shifts in sediment facies (Webster and Davies, 2003). Algal associations throughout reflect shallow water tropical environments.

**96–158 m** – A rhodolith sequence dominated by four rhodolith grainstone horizons, coralline algal grainstones/packstones and two in situ coral framework horizons. The two in situ coral framework horizons represent the oldest reef horizons encountered in the Ribbon 5 core and separate the rhodolith horizon as into an upper and lower section. Changes from coral to rhodolith-dominated horizons are reflected in changes in the coralline algal associations and in one instance at 130 m by a sharp irregular surface and a substantial shift in the  $\delta^{18}O$  record. The algal associations define lower and upper subtropical environments with tropical reef horizons sandwiched between, i.e., the earliest reef growth occurred on a substrate of subtropical rhodolith grainstones.

**158–210 m** – 52 m of alternating grainstones/packstones and packstones/wachestones. The former are comprised of poorly sorted (rudaceous (4 mm) to medium sand) fragmentary corals, encrusting and branching corallines, bryozoans, foraminifers (*Amphistegina*, *Ilerostegina*, encrusting forams), molluscs, serpulids, echinoids, and gastropods: fresh water diagenesis throughout is indicated by interparticle spaces infilled by thick calcite rims, druses, and syntaxial overgrowths while mouldic porosity is developed within molluscs, corals, and especially *Halimeda*. The latter are well sorted, sometimes graded but finer grained (medium to coarse sand) with similar clasts but with up to 50% lime mud dispersed unevenly; little fresh water diagenesis evident. Boundaries between the grainstones/packstones and packstones/wachestones are sharp. Corals are subordinate to coralline algae, of which there are two assemblages, a shallower water *Lithophyllum* assemblage and a deeper water *Mesophyllum* assemblage; both occur today on the warm temperate to subtropical mid- to outer shelf of southern Queensland, south of the Great Barrier Reef (Braga and Aguirre, 1997). The sediments are typical of the same region. The wachestones/

packstones are defined as outer shelf (+60 m water depth) highstand deposits while the grainstones are defined as mid- to inner shelf regressive or lowstand deposits. The relatively sharp boundary between the facies types is, therefore, “event driven” by oscillating sea levels. The fresh water diagenesis is due to exposure in the lowstand effecting the grainstones but not the highstand wachestones/packstones. They are unlikely to represent the debris flows and turbidites postulated by Braithwaite et al. (2004).

### Ocean drilling program site 820

Drilled in 1991, Site 820 forms part of a suite of holes (819, 820, and 821) drilled immediately in front of the Great Barrier Reef in Grafton Passage, east of Cairns (Davies et al., 1991). While Site 821 is considered the most complete sedimentological section, it unfortunately suffers from intense fresh water diagenesis and Site 819 has a major hiatus in the upper part of the section. Site 820 is, therefore, considered to be by far the most complete section and the basis for the interpretations shown in Figure 11c (Davies and Peerdeman, 1998). Three sedimentologic units are recognized:

Unit A 0–65 m composed of wachestones separated by 8 m thick sandy bioclastic packstones composed of planktonic and benthic forams, mollusks, pteropods, minor echinoids, corals, corallines, bryozoans, rhodoliths and *Halimeda*. High and low sedimentation rates reflect alternating high and low sea-level oscillations. Seismic imaging shows aggradation with clear erosional geometries reflecting similar sea-level oscillations.

Unit B 65–145 m composed of wachestones and thin packstone units overlying wachestones and thick packstone units. A major reduction in sedimentation rates coincides with the boundary between Units A+B while alternating high and low rates in Unit B are thought to reflect oscillating sea levels. Seismic imaging shows the upper wachestones and thin packstones to be aggrading packages and the lower wachestones and thick packstones as prograding packages, the boundary occurring at around 110 m in the core.

Unit C – between 145 and 220 m dominated by sandy packstone beds and minor wachestones. An unconformity may occur in this sequence while seismic imaging defines prograding sediment geometries.

In all of the above, there are good agreements between stratigraphic, sedimentologic, and seismic data. However, it is when this data is tied to the isotope data (Figure 11c) that it starts to make sense in terms of the origin of the Great Barrier Reef. Three principal isotopic sequences are recognized:

- (1) Between 0 and 75 m (Unit A above) the signal is dominated by low frequency, high amplitude variation defined by Peerdeman et al. (1993) as related to the orbital eccentricity frequency. This isotopic sequence extends from isotope stage 1–8 and, therefore, has

a base at around 300,000 years. Kroon and Alexander (1993) interpret this signal to indicate a progressive decoupling of surface and bottom water temperatures and raised surface water temperatures.

- (2) Between 75 and 145 m (Unit B above), the signal is characterized by a much higher frequency as well as high amplitude. Peerdeman et al. (1993) interpret this as dominated by the obliquity signal and extending from isotope stage 9–19 at the Brunhes/Matuyama boundary. Davies and Peerdeman (1998) divided the section into two parts (2–1) between 75 and 110 m (isotope stages 9–13) characterized by low frequency high amplitude and (2–2) between 110 and 143 m (isotope stages 13–19) characterized by a much higher frequency and also a high-amplitude signal. These correspond with the division in packstones thicknesses noted above.
- (3) Between 145 and 220 m (Unit C above), the signal is characterized again by a much lower frequency (perhaps dominated by the eccentricity signal) and has high amplitude and as such is similar to the section above 75 m.

Peerdeman et al. (1993) consider the boundary at 75 m as a critical event in the history of the margin. Using the difference between the planktonic O18 signal in the Site 820 core and the benthic O18 signal at the deep sea Site 677 (Shackleton and Hall, 1989), they defined sea surface temperature variation for the northeast Australian margin which showed a substantial rise in temperature of around 3–5°C at around 75 m in the core (around isotope stage 9). This temperature variation corresponds to a change in frequency and amplitude of the isotope signal arising from the change from obliquity to precessional orbital cyclicity. Kroon and Alexander (1993) recognized a similar temperature change at Site 819. Further, Jansen et al. (1986) also recognized a fundamental change in isotope frequency at the 9–8 boundary as defining a change from lower to higher sea surface temperatures leading to the establishment of more interglacial conditions in the period of isotope stages 1–8. At sites 820 and 819, the boundary at 65 m is, therefore, a globally driven change dated at around 300,000 years. Further, the changes defined at the B1/B2 boundary, particularly the change from prograding to aggrading geometries (dated as just prior to 465 ka) reflects a change from shallow to deeper water, coincident with major regional oceanographic reorganization in the Southern Ocean (Kuijpers, 1989; Nelson et al., 1988). The boundary may also mark the change from an obliquity signal to the eccentricity signal seen in Unit A, with Unit B1 representing the transitional warming.

### Relations between Ribbon 5 core and ODP site 820 and implications

The proposed relations and reconciliation of the two data sets are shown in Figure 11a. The profile to the east of Ribbon 5 is one proven by profiling and submersible examination (Phipps et al., 1985). The fundamental change

from subtropical rhodoliths to tropical reef reflects a temperature change and just such a change is seen in the isotopic signal at Sites 820 at a depth of 65 m. The reef section is thus equivalent to Unit A (isotope stages 1–8) and the rhodolith section is equivalent to Unit B1 (isotope stages 9–13). Initial reef establishment of the coral frameworks in the middle of the rhodolith section must, therefore, date at sometime after 465 ka while the firm establishment of the main reef section above 96 m dates from around 300,000 years. The six stacked reefs at Ribbon 5 correspond to sea-level highstand growth phases, the first being either stages 8 or 9. The rhodolith section, equivalent to B1, represents the transitional warming suggested by the change in the obliquity signal noted above. This would be equivalent to conditions operating today to the south of the Great Barrier Reef on the south Queensland shelf (Davies et al., 1991). Further the sea-level oscillations defined by the wachestone/packstone alternations at Site 820 and representing warming and cooling episodes, serve also to explain the reef intercalations within the rhodolith sections. Davies and Peerdeman (1998) propose that the facies variations on that shelf and their lateral migration during oscillating sea level, define a model for the sub-reef rhodolith section at Ribbon 5 and explain the reef frameworks within that section.

### Cross-shelf growth of the great barrier reef

Once established in the shelf edge zone, is it right to assume that reefs quickly spread everywhere on the shelf? The results of a second borehole at Boulder Reef (Figure 11b) on the inner shelf and drilled during the Ribbon 5 campaign suggest otherwise. Four stacked reef sections (R1–R4 in Figure 11b) sit on siliciclastic mud and clay foundations at a depth of 34 m. The siliciclastics extend to 86 m where drilling terminated; however, coral-bearing units (R6 and R5) lacking a true framework occur within this mud section and have been interpreted as low-diversity coral communities reworked to form a rubble (Webster and Davies, 2003). Their presence is, however, significant. The base of the core has been tentatively dated by ESR as  $210 \pm 40$  ka, which suggests that the beginning of reef growth on the inner shelf was much later than on the outer shelf. Two failed attempts (R5 + R6, Figure 11b) were followed by the establishment (R4) of a reef structure, after which Boulder Reef was reestablished on three later occasions. The two failed attempts at 55 m (R5) and 63 m (R6) and the beginning of the main reef section (R4 at 34 m) occurred on siliciclastic foundations, testifying to the fact that the inner shelf was a turbid environment during highstands, perhaps more turbid than today. It is concluded, therefore, that the pre-reef environment was totally different on the inner shelf compared with the outer shelf and that reef initiation was later on the inner shelf compared with the outer. In both cases, however, reef growth was a relatively recent phenomenon.

The drill core at Ribbon 5 and Boulder Reefs testify to the youth of the Great Barrier Reef and to the fact that reefs

have been destroyed and regrown again on at least six occasions on the outer shelf (Figure 11a, R1–R6) and four occasions on the inner shelf (Figure 11b, R1–R4). Coupled with the isotopic data from the ODP cores, it is concluded that sea-level oscillations are the cause of the repeated demise and subsequent reestablishment. Further, the isotopic data also indicate that the initial establishment of the reefs on the outer shelf was climate controlled, and occurred on a rhodolith-dominated bank on the outer shelf. Such subtropical red algal banks may have formed in the way such banks occur on the south Queensland shelf today.

### The modern reef

The history of growth and development of the modern reef has been defined largely by drilling through the reefs into their Pleistocene substrate. Hopley et al. (2007) report 160 drill holes in 50 reefs, and 750 dates. These data indicate that the amount of Holocene reef growth varies from 0 to 28 m (Davies and Hopley, 1983; Hopley et al., 2007). Transects across the northern reefs east of Cooktown and off Townsville indicate little difference in the thickness of reef from west to east (Davies et al., 1985). Longitudinally, however, down the length of the Great Barrier Reef, Hopley et al. (2007) report an increase in thickness from Torres Strait to south of Cairns and then a gradual decrease in thickness to the south. They, therefore, imply a change in the depth of the Pleistocene substrate from north to south and invoke either long or short-term subsidence to explain it. An additional process, hydroisostasy, has also been at work to ultimately define systematic variations in thickness (see *Glacio-Hydro Isostasy*, this volume).

The composition of the Pleistocene substrate has been shown to be reef framework on the mid- and outer shelf, similar or identical to the modern reef. The Pleistocene corals are, however, sometimes accompanied by thick coralline algal crusts and *Halimeda* grainstones as seen at One Tree Reef and Ribbon Reef 5 (Marshall, 1983; Webster and Davies, 2003). On fringing reefs, the Pleistocene is sometimes composed of mud, sand, and gravel (Kleypas and Hopley, 1993). Soil horizons have been reported from Fairfax and Fitzroy reefs in the southern Great Barrier Reef, from Redbill, Hayman, and Davies Reefs in the central region and from Ribbon Reef 5 in the northern region. Soil development implies erosion of the underlying limestone and it is surprising that so few have been reported considering the number of holes drilled. As the age of the Pleistocene substrate has been established in the south at One Tree Reef (Davies and Marshall, 1980; Marshall, 1983) and in the north at Ribbon Reef 5 (International Consortium for Great Barrier Reef Drilling, 2001) as isotope stage 5 (around 125 ka), then sea level is likely to have been +5 m above present sea level. Assuming the stage 5 reef grew to sea level, erosion of up to 33 m must have occurred on reefs in the region (assuming no subsidence). Allowing for

subsidence of 10 m (rapid) in the 100 ka period since exposure of the 125 ka reef, then erosion of up to 23 m will have occurred. The Pleistocene surface on which the Holocene reef has grown is, thus, a much modified (some would say karstified) earlier reef.

### Holocene reef start-up

Holocene sea level in the Great Barrier Reef transgressed the foundations of most Pleistocene platforms in the time frame 7–10,000 years BP (Hopley et al., 2007). Start-up growth occurred after transgression was complete, with 17 out of 22 reefs dated starting growth in the time frame 7,100–9,000 years BP. On the outer shelf start-up began at 6.6–8.6 years BP; in the mid-shelf it was around 9.1–6.9 years BP, while on the inner shelf it was around 7.8–6.3 years BP.

In the Great Barrier Reef, sea level changed from a transgressive to a stillstand condition around 6,500 years BP. The age at which reefs reached sea level broadly depends on the depth of their foundations and these ages are summarized in Hopley et al. (2007). Nearly 60% of all reefs cored and dated reached sea level in the interval 5,000–6,500 years BP meaning that nearly 60% of the reefs studied have been subject to a shallow water energy regime for most of the time that they have been growing. Growth, therefore, must reflect this.

The interactions between growth and sea level prompted Davies and coworkers (Davies and Montaggioni, 1985; Davies et al., 1985) and Neumann and Macintyre (1985) separately, independently, and in different oceans to define five strategies of reef growth in the Holocene:

- Keep-Up Reef growth – reefs growing and keeping pace with sea-level change, such that reef flats developed early. Pleistocene foundations are relatively shallow.
- Katch-Up 1 Reef growth – reefs which started to grow well after inundation but then grew so quickly that they were able to catch-up before sea level stabilized.
- Katch-Up 2 Reef growth – reefs which started to grow well after inundation but did not grow so fast so that catch-up occurred after sea level had stabilized.
- Katch-Up 3 Reef growth – reefs which did not start to grow until after sea level had stabilized so that the growth was into continually shallowing water.
- Screwed-Up (Give-Up) Reef Growth – reefs which died before reaching sea level. Neumann and Macintyre (1985) considered that these were “drowned reefs,” but Davies and coworkers considered other factors could also effect death (turbidity, elevated nutrients, and subsidence).

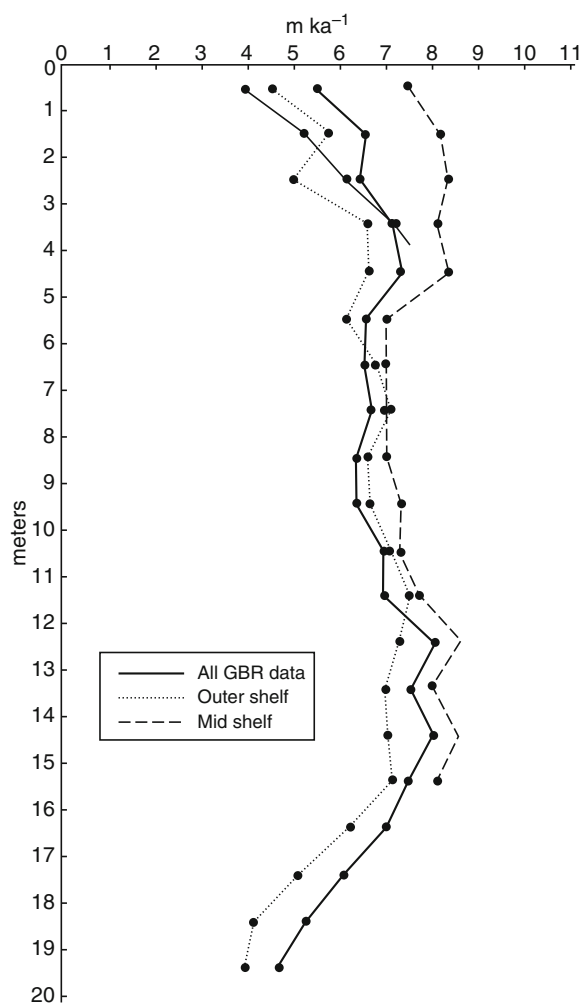
More than one growth strategy can occur on the same reef as local environment factors affect the growth response (Davies and Montaggioni, 1985; Davies et al., 1985). Further, the rates of growth are depth dependent; thus growth approximates an “S” shaped curve – slow growth to start, rapid growth as the reef grows into shallow water and slow growth again as the reef is subject to high energy in shallow water. Plots of growth rates against paleo-water



depths (Davies et al., 1985) show rates of  $>8 \text{ m/ka}^{-1}$  for water depths of 12–15 m,  $4 \text{ m/ka}^{-1}$  for water depths of 20 m and corresponding low rates in shallow water. This is particularly well seen for the outer shelf reefs and total reef data set in Figure 12. It is not so well seen for the mid-shelf reefs where the shallow water rates of growth are not that much less than the mid-water-depth rates but this may be due to the reduction in energy on the mid-shelf reefs compared to the outer shelf reefs. Surprisingly, growth rates change little with latitude.

### Growth at sea level

When a reef reaches close to a stabilized sea level, it comes under the influence of the ambient hydrologic regime. Three features are produced on most reef types (see below) – the algal and coral reef flat and the sand sheets: rubble flats are found on only a few reefs. The reef flats and the rubble flats are described in detail by Thornborough



**Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 12** Vertical growth rate data plotted against palaeo water depths (modified after Hopley et al., 2007).

and Davies (Reef flats this volume). Attention is given here, therefore, to the sand sheets which are intertidal and subtidal. In Figure 13, intertidal sand sheets occur on the southern reef flat bordering the lagoon while subtidal sand sheets occur between the rubble banks and the lagoon along the eastern margin. The southern intertidal sand sheet occupies an area of  $822 \times 1,000 \text{ m}^2$  and contains a sand volume of 14 million tones of carbonate. A section through the sand sheet summarizes its major growth features as seen in vibrocores and drill holes and surface maps show its essential granulometric variations (Figure 13c). In Figure 13b a lower subtidal sand overlies rubble close to the junction with the coral flat and is in turn overlain by intertidal sands as the body builds up to sea level. The sand is derived from the windward margin and the outer edge of the coral flat from where it is wave transported on every tide toward the lagoon. The sediments of both units comprise corals, coralline algae, foraminifera, mollusks, and minor *Halimeda*. The subtidal sands are characterized by fining upward rhythms while the upper intertidal sequences are characterized by coarsening upward sequences. However, in both units most stratification is destroyed by shrimp bioturbation. The intertidal sand sheets are prograding into (filling up) the lagoon.

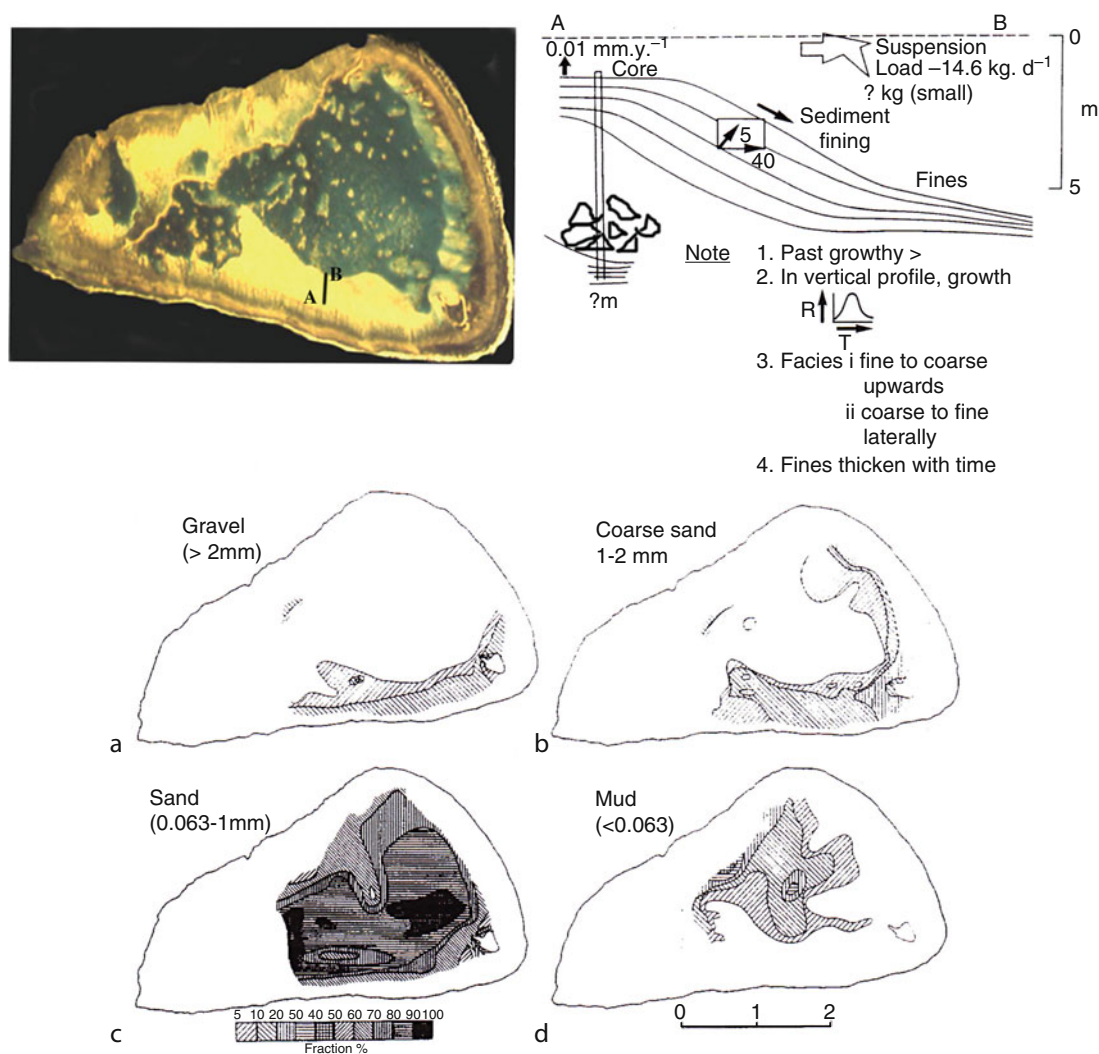
The eastern subtidal sands occur in 3–5 m of water along the eastern junction of the lagoon with the eastern rubble flat (Figure 13a). Surface sediments are very coarse to fine sands and show a decrease in grain size toward the lagoon; cores show fining upward sequences being destroyed by bioturbation. These subtidal sands occupy an area of  $538,000 \text{ m}^2$  and contain approximately 9 million tones of carbonate. They are comprised of uncemented corals, gastropods, foraminifera, corallines, and bivalves derived through bio and physical erosion of the eastern rubble flats.

The distinctive sea-level signatures on almost all reefs in the Great Barrier Reef are the algal/coral flats and sand sheets. Rubble flats occur on only the high energy reefs.

### Types of reefs

The following reef types have grown in the Great Barrier Reef – fringing reefs, mid-shelf reefs (patches, crescentic, lagoonal platform reefs, and flat-topped planar reefs), and outer shelf reefs (detached reefs, deltaic reefs, ribbon reefs, and giganto-reefs) (Maxwell, 1968; Hopley, 1982). For completeness, they are briefly described below. (See entries *Reef Classification by Hopley (1982)*; *Reef Classification by Maxwell (1968)*).

According to Hopley et al. (2007), there are 758 fringing reefs in the Great Barrier Reef Marine Park, but representing less than 2% of the total reef area. Most occur between latitudes 20–22S and most fringing reefs show a weak biologic and morphological zonation. Recent studies describe fringing reefs in turbid inner shelf environments (Perry and Smithers, 2009; Smithers et al., 2006) comparable to the environments postulated above for Boulder Reef off Cooktown.



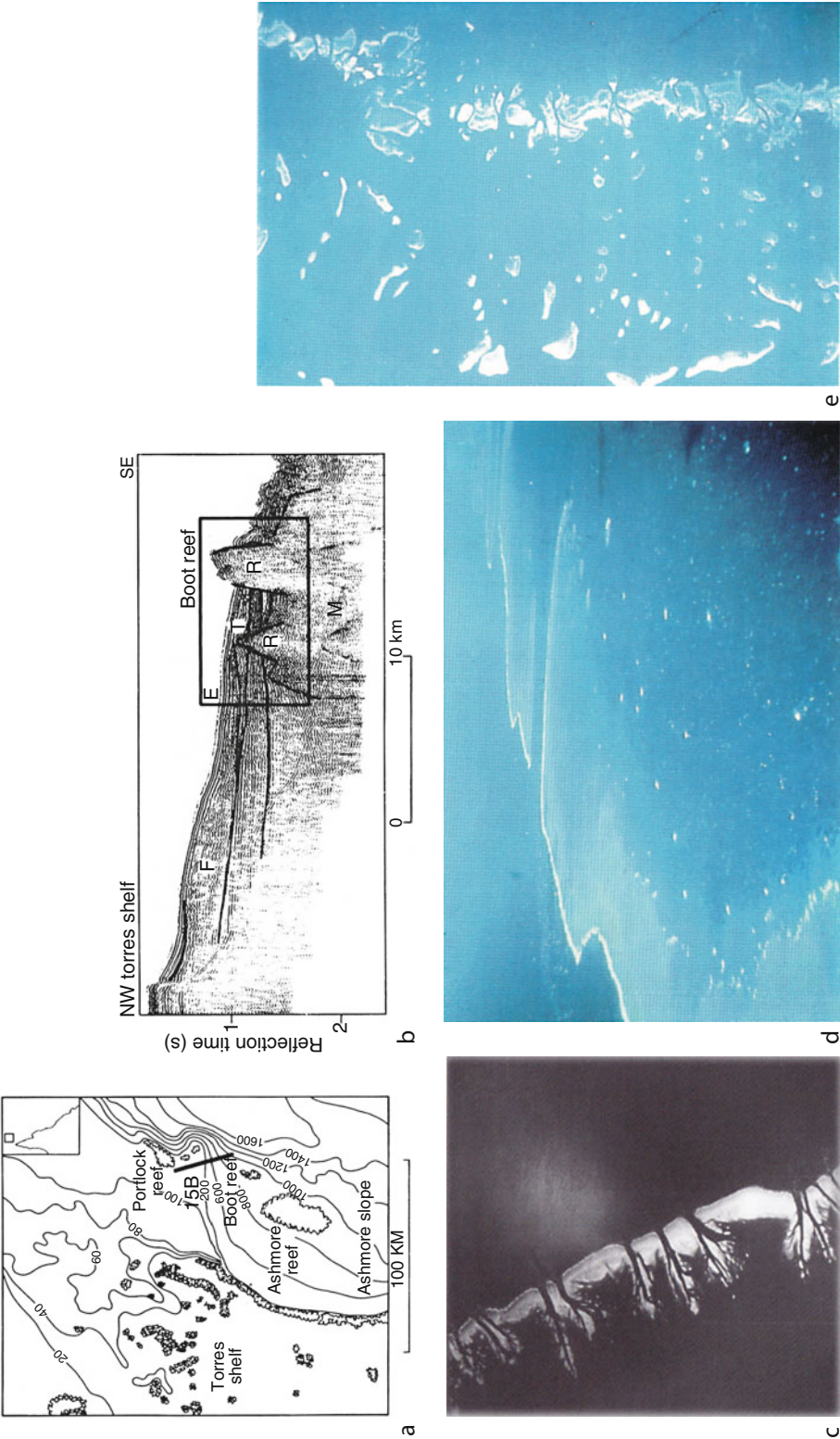
**Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 13** (a) Vertical air photograph of One Tree Reef in the southern region. (b) Section through the sand sheet summarizing its major features, and (c) granulometric variations across the sand sheet and lagoon.

Mid-shelf reefs occur throughout the Great Barrier Reef region although the number, shape, and complexity varies substantially. On the basis of size and physical attributes, they are classified as patches, crescentic, lagoonal platforms, and flat-topped planar reefs. Juvenile, mature, and senile varieties of the crescents, lagoonal, and flat-topped reefs have been described (Davies, 1983; Hopley et al., 2007). Critical factors in their evolution are size, depth, and shape of the Pleistocene substrate; the length of time they have been at sea level; and the energy in the shallow water environment.

Outer shelf reefs occur on the shelf edge and are often linear, and aligned parallel to the edge which can be steep or stepped. Detached reefs occur in the northern region eastward of the main reef edge (and therefore detached), particularly east of the Torres Shelf where the Ashmore-Boot-Portlock complex occurs (Figure 14a). They have

grown on pinnacles of continental crust and are fronted by very deep water in excess of 1,000 m, while the moat between the reefs and the shelf edge can be up to 700 m deep and infilled with prograding siliciclastics from the Papuan platform (Figure 14a). Deltaic reefs also occur in the extreme northern region and are made up of short narrow reef segments separated by passes behind which distinctive delta-like patterns have been produced by tidal currents flooding through the passes and on which reefs have grown mimicking the delta-like shapes of the underlying sand substrate (Figure 14b).

Ribbon reefs occur on the shelf edge over a distance of 700 km between 11S and 17S as a series of narrow discrete reefs (10–28 km long) separated by passes up to a kilometer wide. They are numbered sequentially northwards. Probably the best known of the Ribbons is Ribbon 5 (Figure 14c) because there are three drill holes



**Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 14** (a) Seismic sections across the Ashmore – Boot-Portlock reef complex (b) the northern deltaic reefs (After Hopley et al., 2007), (c) Ribbon reefs of the Pompey Reef complex (After Hopley et al., 2007).

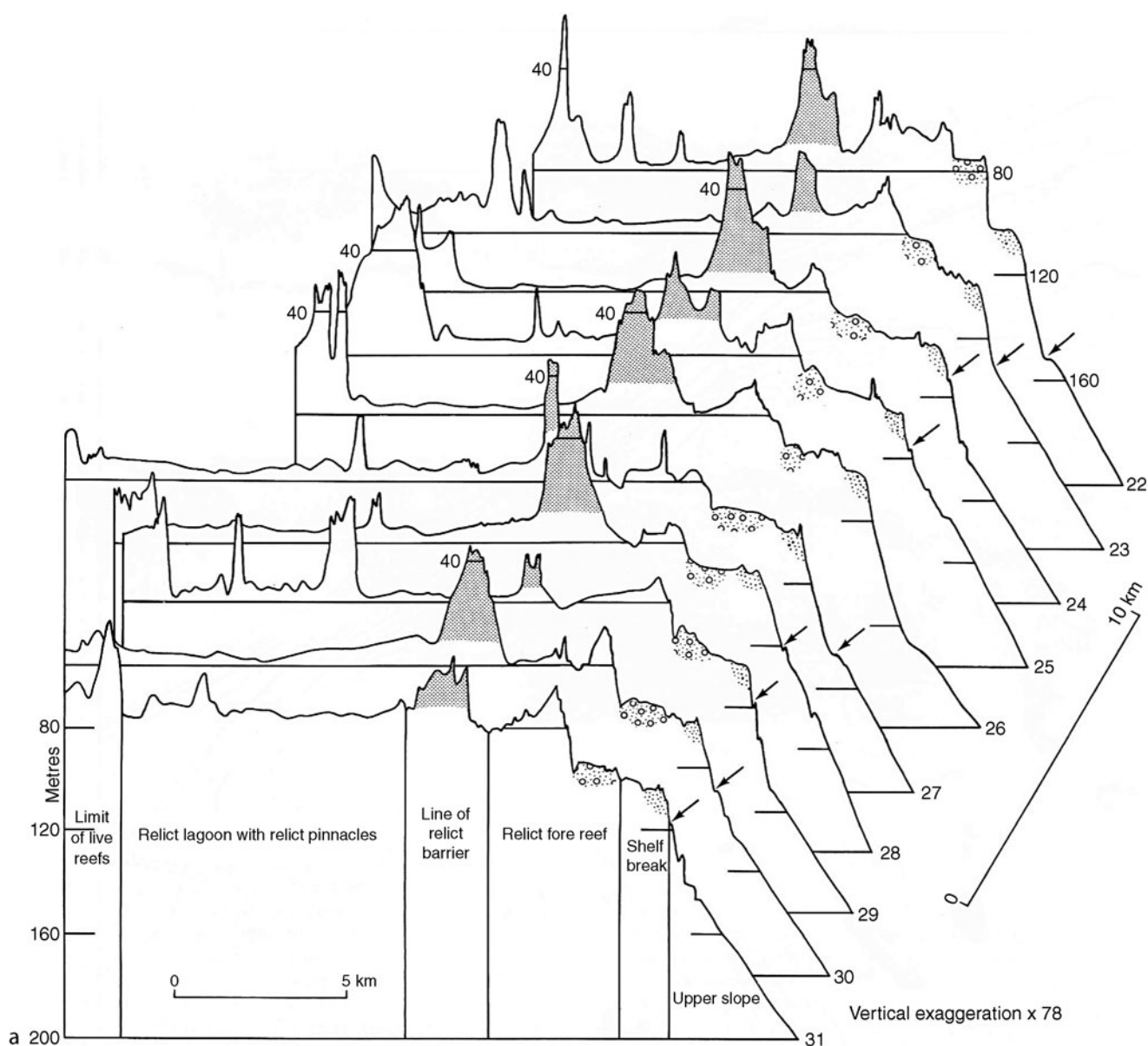


through the Holocene and the deep hole through the total thickness of the Great Barrier Reef (Davies et al., 1985; Webster and Davies, 2003) reported above. The gigantoreefs of the central southern region (Pompey Reefs) are indeed large (Figure 14d). Forming an almost continuous barrier over a shelf edge length of 140 km, many of the reefs are 50–100 km<sup>2</sup> in area, and 15 km long (Hopley, 2006; Hopley et al., 2007). They are surrounded by water depths of 60 m and oceanwards give way to a terrace sloping down to a shelf edge at 100 m. The morphology of this terrace is shown in Figures 14b and 15.

### Growth – the facies produced

Five broad carbonate facies are recognized as occurring in the Holocene reefs of the Great Barrier Reef. Three are framework facies and two are detrital facies:

1. Coralline algal facies are laminated crusts, often centimeters thick, and/or encrustations on branching or massive corals, composed principally of *Mastophoroid* algae either *Hydrolithon onkodes* or *Neogoniolithon fosliei*. Vermetid gastropods and encrusting foraminifera are constant faunal associates. The facies is best



Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 15 Bathymetric profiles across the submerged shelf east of Hydrographer's Passage (From Harris and Davies, 1989).

developed on windward margins, but encrusting coral-lines coat most dead or dying surfaces in all intertidal reef environments.

2. Branching coral facies is comprised essentially of various species of *Acropora*, *Pocillopora*, and branching *Porites*. Growth form varies with depth, light, and energy. In shallow water, variations in energy define wide differences in species composition and diversity. Water-depth changes produce similar compositional variations.
3. Massive (Head) coral facies is comprised mainly of various species of *Porites*, *Goniopora*, *Favia*, *Leptoria*, *Platygyra*, *Symphyllia*, *Leptastrea*, *Goniastrea*, and massive *Acropora*. As with the branching forms, water depth and energy defines diversity.
4. Sand facies is usually medium to coarse sand comprising coral, corallines, benthic foraminifera, and minor *Halimeda*. Occasionally rudaceous-sized fragments are found. Sorting varies depending on distance from source and degree of bioturbation. It forms large sand sheets between coral flats and lagoons and also infills lagoons.
5. Rubble facies is comprised of massive, platey, and branching corals varying in size from 20 kg blocks to finger-like sticks. They are poorly sorted, occupying large intertidal areas, sometimes cemented, often bioeroded; also found in spurs and grooves, and at the base of lagoonal patch reefs. They are produced either by in situ collapse (in lagoons) or by energy-related breakage and transport.

Two non carbonate facies have also been identified but are minor compared with the carbonate facies. These are siliceous muds and clays derived from rivers inputting onto the inner shelf (Davies and Hughes, 1983; Smithers and Larcombe, 2003), and granites as at Lizard Island contributing coarse quartz and feldspar to an otherwise carbonate environment, but with corals actually growing on the granites (Webster, 1994).

### Growth models

Three growth models are presented below for three distinctive reef types defined above as lagoonal platforms, crescent reefs, and ribbon barrier reefs.

#### The One Tree Reef Model

One Tree Reef (Figure 13) occurs in the Capricorn and Bunker Reefs of the southern Great Barrier Reef. Surface sampling and subsurface drilling and coring define One Tree as the best understood reef in the whole region. Three dimensional models show the Holocene One Tree Reef growing atop its Pleistocene foundation and mimicking its shape. In Figure 16a, the Pleistocene is exposed during the lowstand. The highest part of the exposed rim is the algal flat and coral flat because the areas of greatest erosion during the lowstand would likely be the reef front and the sand flat/lagoon margin (see *Antecedent Platforms*, this volume). Transgression would initiate growth on the high rim, after which growth would be to sea level

(Figure 16b). At this point, development of the reef flat, sand sheets, lagoonal patch reefs, and the rubble sheets will grow to the stable sea-level position (Figure 13a). The effect of dominant energy is to produce clear constructional and destructional windward/leeward aspects. Throughout its history different parts of One Tree exhibited keep-up or catch-up strategies.

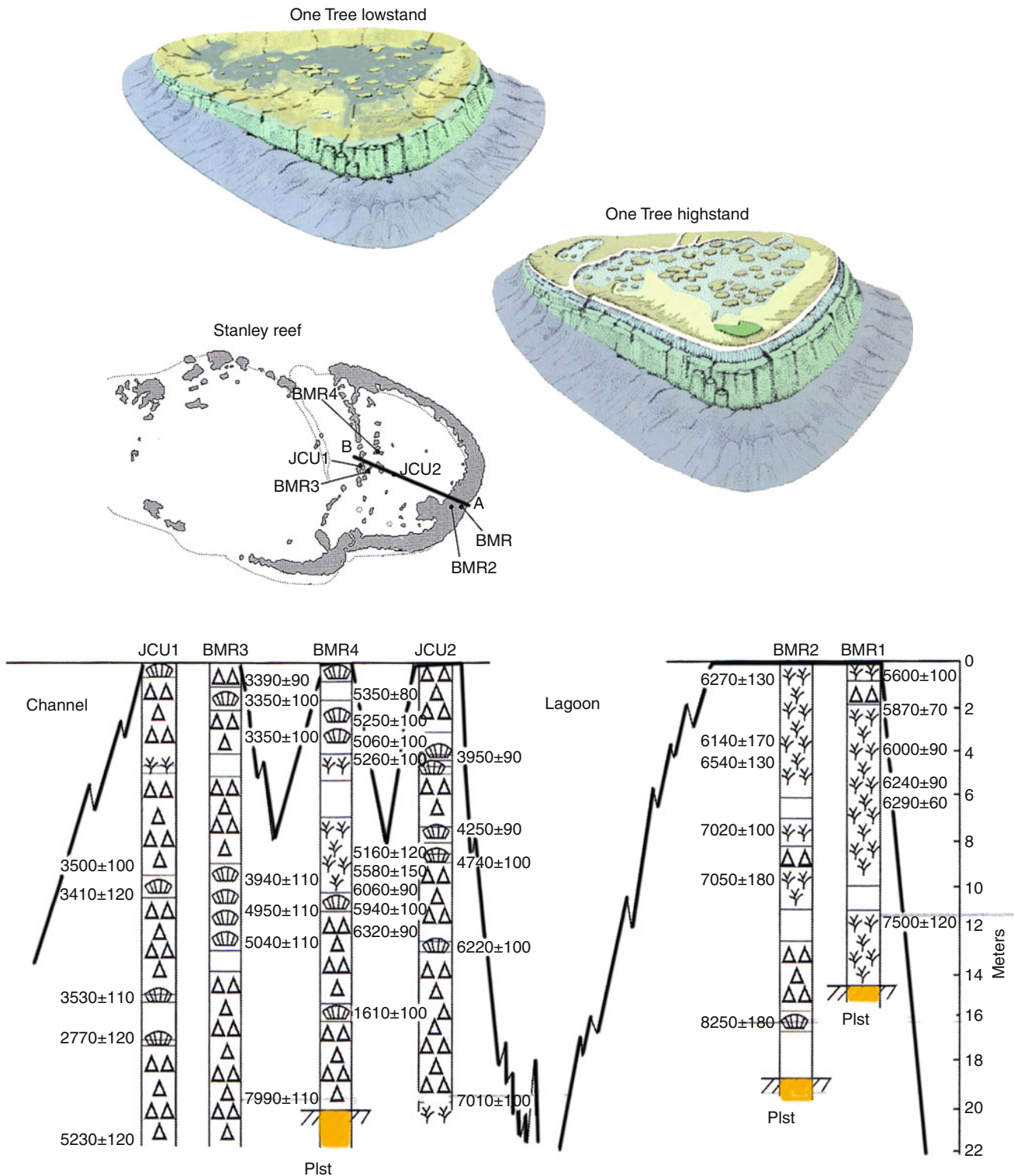
#### The Stanley Reef Model

Stanley Reef (latitude 19.18S) is a crescent reef in its eastern part and an “almost-atoll” in the west (Figure 16c). All work conducted was on the eastern part which is both similar and very different to One Tree Reef; similar in having a distinct edge to the east and southeast and dissimilar in having a wide open lagoon and a lee edge which is patchy. The reef is highest around the rim along the eastern margin where the Pleistocene is at nearly 15–18 m and on the leeward patches at 20–22 m. A lagoonal patch reef in a lee position showed the Pleistocene at around 20 m. The lagoon is currently deep (+20 m), and assuming 5–10 m of sediment, the Pleistocene in the lagoon would be at a depth of +30 m. During low sea level, Stanley was a crescent with a high eastern rim decreasing in height to the west, and a large open deep basin on the site of a former lagoon and open lee end. Holocene growth on this antecedent surface occurred almost simultaneously on windward and leeward margins (Table 1). At the time of the first dated growth, palaeowater depths on the windward margins were 10–12 m and on leeward edges 14–18 m. The first phase of growth was vertically to sea level, after which, growth of the windward margin replicates that seen on most reefs (see One Tree and Ribbon 5) with the development of a windward reef flat and sand flat. The leeward edge arrived at sea level later than the windward margin. The next phase of growth for this crescent reef is for the leeward patches to coalesce to form a continuous lee edge, at which time, the crescent reef will become a lagoonal platform reef. At this stage, most sediment derived from the windward margin will be trapped in the lagoon leading to an acceleration in the infill of the lagoon (assuming enough time).

#### The Ribbon 5 model

Ribbon 5 (Figures 11a and 17) is a shelf edge barrier reef east of Cooktown for which the database is more complete than any reef in the Great Barrier Reef. It defines both the Pleistocene and the Holocene evolution. The model, defined by data in Figures 11a and 17, has the following elements:

1. Initiation of reef growth on a shelf edge rhodolith bank following a major climate change around 300,000–350,000 years BP.
2. Destruction and regrowth of reefs successively, due to sea-level oscillations, on eroded antecedent surfaces with each reef initiating and growing on or close to the position of the previous reef. A stacked succession of reefs is thus formed (Figure 17b).



**Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 16** (a) Low stand position shows the pedestal on which One Tree Reef sits. (b) high stand growth of One Tree Reef on its pedestal and (c) Stanley reef - a mid shelf reef in the central reef region. The lithologies encountered in drill holes indicate a framework-dominated windward margin and a sand dominated lee margin. Plots of depth against age show the windward margin getting to sea level first and progressively later backwards.



**Great Barrier Reef: Origin, Evolution, and Modern Development, Table 1** Oldest drill dates and depths from Stanley Reef and calculated sea-level and water depths

| Drill hole | Oldest age | Depth | SL position | Water depth |
|------------|------------|-------|-------------|-------------|
| BMR 1      | 7,500      | 12 m  | −2m         | 10 m        |
| BMR 2      | 8,250      | 16 m  | −4m         | 12 m        |
| BMR 3      | 7,990      | 19 m  | −5m         | 14 m        |
| JCU 2      | 7,010      | 19 m  | −1m         | 18 m        |

- Growth of the Holocene reef occurred first on the windward margin (6,500–7,000 BP) on a Pleistocene substrate at around −15 to 16 m, and progressively later leewards where the oldest date for growth is around 4,500 BP at a depth of about −14 m. The windward margin began to develop its reef flat and shed sand leewards after reaching sea level around 6,000 BP. The leeward margin holes (holes 3 + 4) are dominated by sands which postdate the time at which the windward margin approached sea level.
- Growth of the Ribbon reefs since sea level stabilized has been due to (1) catch-up to sea level by patch reefs that initiated late, and (2) leeward growth of the coral flat (as described for One Tree in Reef Flat Thornborough and Davies this volume), and substantial backward shedding of sand into the leeside environments.

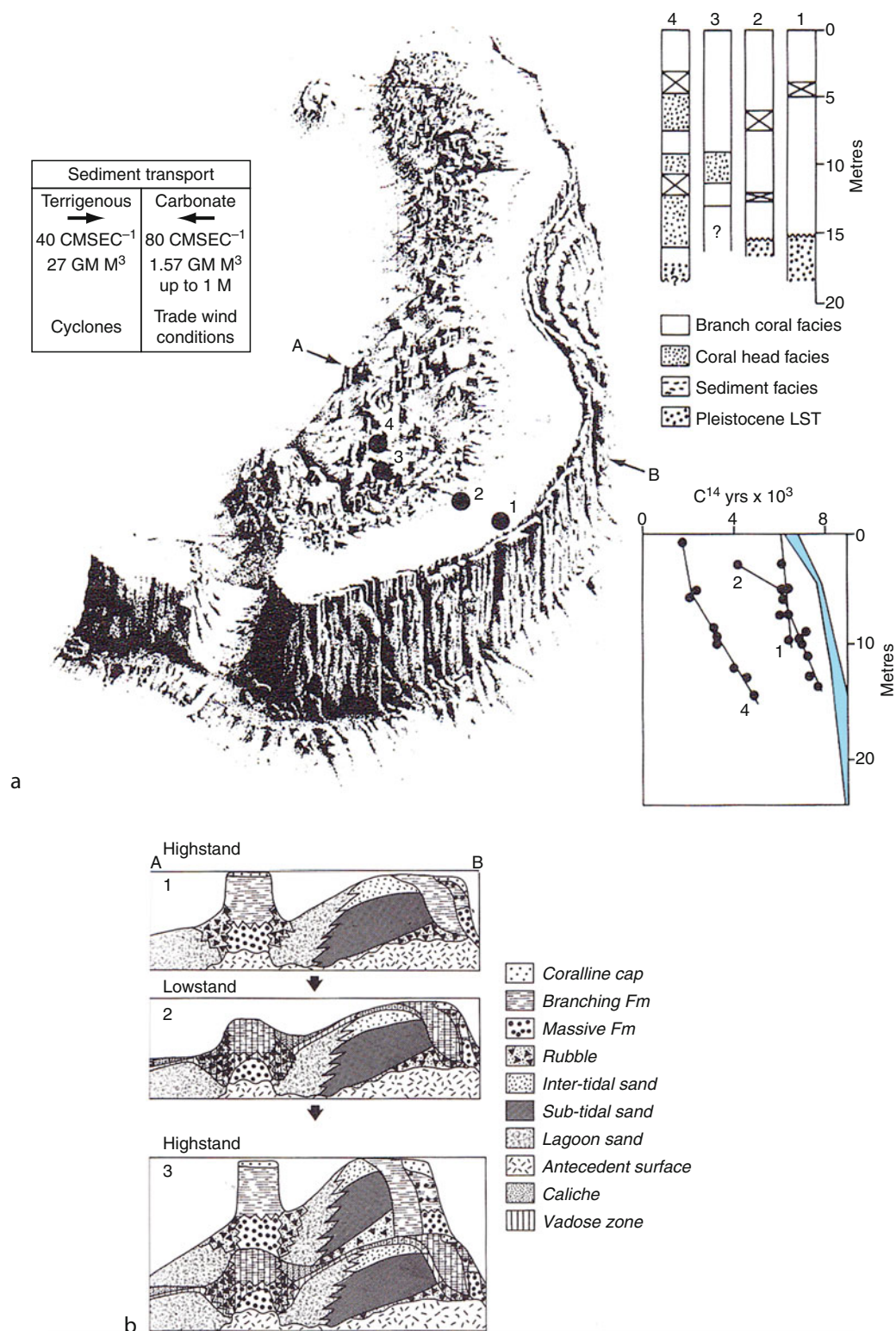
Most reefs in the Holocene, with the possible exception of fringing reefs, have undergone the same basic processes of growth from an antecedent platform to sea level and then growth controlled by the direction and energy of the impinging energy. This is common in the three models defined above. The models are however of two totally different reef growth environments – the shelf edge and the mid-shelf platforms. They are almost two end members with different characteristics produced by the same parameters. In both cases the dominant control is substrate, to produce a linear outer shelf feature and crescentic/lagoonal mid-shelf features. However, in the mid-shelf reefs, Davies (1978), Davies and Marshall (1980), Hopley (1982), Davies (1983), and Davies and Hopley (1983) all recognized patterns of reef development with specific characteristics which appeared to overlap and which could be related to the depth, size, and shape of the Pleistocene substrate, the timing of reaching sea level, and the total energy within the physical environment. Hopley (1982) and Hopley et al. (2007) show similar models for the central reefs. In an evolutionary sense, reefs can be judged to be juvenile, mature, and senile. Thus, crescentic reefs (Stanley, Fitzroy) can grow into lagoonal platform reefs and eventually into flat-topped platforms with live coral growth only around the perimeter. Most importantly, the rate of progress along the evolutionary chain is a function of the size and depth of the platform and the energy impinging in the stillstand system. Thus, small reefs (Wreck in the Capricorns) will progress to senility rapidly while Stanley is yet to achieve maturity. The three reef

types will however be dominated by both different processes and the same processes acting at different rates. This becomes an important issue when considering how reefs will react to climate changes proposed for the next 50 years. As a consequence, for example of increased storminess, mature reefs (and most are) will progress more rapidly to senility in spite of (or rather because of) possible increases in growth potential in areas which are not temperature marginal. The same conditions affecting a senile reef will accentuate erosion leading to possible obliteration of such reefs, particularly if they are small in size.

## Summary

The Great Barrier Reef occupies the passive margin of northeast Australia, and is arguably the largest coral reef system to have ever existed on the planet. It represents one of a series of major architectural features forming the margin – the Eastern, Queensland and Marion Plateaux; the Pandora and Bligh Troughs; the Osprey Embayment; and the Queensland, Townsville, and Cato troughs. Coral reefs occur on all three plateaux in addition to the Great Barrier Reef. Some 3,600 reefs are estimated to form the Great Barrier Reef. The margin architecture seen today is a consequence of rifting, drifting, subsidence, sea-level/climate change, and continental collision. Coral reefs established on three occasions (1) in the early to late-mid-Miocene; (2) in the uppermost Miocene; and (3) in the Pleistocene. The Great Barrier Reef, as it is known, started in the late Pleistocene, as seen in drill core data from Ribbon 5/Boulder Reefs and at ODP site 820. On the outer shelf at Ribbon 5, drill core data show a reef section (0–96 m) above a rhodolith-dominated section (95–158 m) above a packstone/wachestone section (158–210 m). Initial reef establishment of the coral frameworks in the middle of the rhodolith section dates from some time after 465 ka while the firm establishment of the main reef section above 96 m dates from around 300,000 years. At Boulder Reef on the inner shelf, tentative dating places reef start-up at around 210,000 years. Reef initiation is therefore most probably facies controlled and not karst antecedent controlled. The ages and the succession of reefs at Ribbon 5 (six reefs) and Boulder Reef (four reefs) also testify to the fact that reefs have been destroyed and re-grown again on at least six occasions on the outer shelf and four occasions on the inner shelf. The modern Great Barrier Reef is the last expression of regrowth following the last post-glacial transgression. Almost certainly, antecedence has assumed greater relevance through each new growth phase.

The development of the modern reef system is documented through the largest geoscientific reef database for any system in the world (160 drill holes in 50 reefs and 750 dates). Start-up occurred 7–10,000 years BP most often on eroded (karstified) remnants of the previous (125 ka) reef phase. Nearly 60% of all reefs cored and dated reached sea level in the interval 5,000–6,500 years BP meaning that nearly 60% of the reefs studied have been



**Great Barrier Reef: Origin, Evolution, and Modern Development, Figure 17** Ribbon Reef 5 (a) Three dimensional model of Ribbon 5 down to about 25 m and showing the lithologic and radiocarbon dates from drill holes (1–4). (b) The distribution of facies developed in a high energy reef system as a function of successive sea-level oscillations. Facies variations within the successive reefs show backward prograding sedimentological and biological wedges.

subject to a shallow water energy regime for most of the time that they have been growing; growth therefore reflects this. Different reef growth strategies reflect the interaction of substrate depth, sea-level rate of change, and coral growth rate. A major change in growth and bio- and sedimentary facies occurs when the growing reef approaches sea level – the formation of algal and coral flats reflect biofacies changes and sand sheets and rubble flats reflect sedimentary facies changes.

Five broad carbonate facies are recognized; three are framework facies and two are detrital facies:

1. Coralline algal facies. These are laminated crusts, often centimeters thick and/or encrustations on branching or massive corals. The facies is best developed on windward margins, but encrusting corallines coat most dead or dying surfaces in all intertidal reef environments.
2. Branching coral facies. Growth form varies with depth, light, and energy. In shallow water, variations in energy define wide differences in species composition and diversity. Water-depth changes produce similar compositional variations.
3. Massive (head) facies. As with the branching forms, water depth and energy define diversity.
4. Sand facies. These are usually medium to coarse sand comprise coral and corallines, benthic foraminifera, and minor *Halimeda*. Forms large sand sheets between coral flats and lagoons and also infills lagoons.
5. Rubble facies. These are comprised of massive, platy, and branching corals. Produced either by in situ collapse (in lagoons) or by energy-related breakage and transport.

Three growth models are presented, two for mid-shelf platform reefs (One Tree and Stanley Reefs) and one for outer shelf barrier reefs (Ribbon 5). It is concluded that most Holocene reefs in the Great Barrier Reef, with the possible exception of fringing reefs, have undergone the same basic processes of growth from an antecedent platform to sea level and then growth controlled by the direction and energy of the impinging energy. This is common in the three models defined above. The models are however of two totally different reef growth environments – the shelf edge and the mid-shelf platforms. They are almost two end members with different characteristics produced by the same parameters. In both cases, however, the dominant control is substrate, to produce a linear outer shelf feature and crescentic/lagoonal mid-shelf features. However, in the mid-shelf reefs, patterns of reef development are recognized which have specific characteristics which appear to overlap and which are probably related to the depth, size, and shape of the Pleistocene substrate, the timing of reaching sea level, and the total energy within the physical environment. In an evolutionary sense, reefs can be judged to be juvenile, mature, and senile. Thus, crescentic reefs may grow into lagoonal platform reefs and eventually into flat-topped platforms with live coral growth only around the perimeter. Most importantly,

the rate of progress in this evolution is a function of the size and depth of the platform and the energy impinging in the still stand system. Thus, small reefs (Wreck in the Capricorns) will progress to senility rapidly while Stanley (large reef) is yet to achieve maturity. Evolutionary progression may occur through more than one highstand growth phase. Predicted future climate changes will accelerate evolutionary progression.

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## Cross-references

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## HALIMEDA

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### Synonyms

*Siphonales* (in older literature); *Siphonous* algae

### Definition

*Halimeda* is a genus of warm temperate to tropical macroalgae classified into

Phylum: *Chlorophyta*  
Class: *Bryopsidophyceae*  
Order: *Bryopsidales*  
Family: *Halimedaceae*  
Genus: *Halimeda*

### Phytochemistry

#### Photosynthetic pigments

*Halimeda* chloroplasts contain the characteristic photosynthetic pigments of the Chlorophyta, plus *siphonoxanthin* and *siphonoin*, which are specific to the Bryopsidales.

#### Cell wall

*Halimeda* and most other Bryopsidales have cell walls composed of a **xylose-based  $\beta$ -1–3 linked xylan**, not the glucose-based cellulose found in all other Chlorophyta.

#### General

Author's *Halimeda* Web site:

<http://members.iinet.net.au/~edrew1/halimeda/halimeda.htm>

### Appearance

*Halimeda* thalli are composed of branching chains of calcified green segments joined together by flexible, uncalcified nodes. The thalli may be erect, pendant, or sprawling. They may grow up to 25 cm high or cover over 1 m if sprawling. They are anchored by holdfasts, which may be

- (i) A small basal mass about a cm long, consisting of matted rhizoidal filaments adhering to rocks.
- (ii) Or a large, dense bulbous mass, 1–13 cm long, buried in the sediment. It consists of fine rhizoids with adhering sediment particles and can be up to 40% of the plant's total weight.
- (iii) Or several diffuse, inconspicuous patches of rhizoids arising at intervals from segments or nodes of the algae sprawling on rocks or unstable surfaces.

Segment size and shape vary considerably between species. They may be flat, keeled, or even cylindrical in some. Their outline varies from ovate to cuneate and may be distinctly lobed. The width varies from 2 to 55 mm.

### Taxonomy

*Halimeda tuna*, from the Mediterranean Sea, is the holotype of the genus. It was first described, but named *Sertolara*, by Imperato (1599). During the next century, it was given several different generic names and was considered to be a coralline animal. In 1812, it was finally recognized as a plant and given its currently recognized binomial name, *Halimeda Tuna* (Ellis and Solander, 1786; Lamouroux, 1816). At that time, exploration of tropical regions had just begun, and the number of described *Halimeda* species reached 26 by 1887, most species being described solely on the basis of their segment morphology.

Currently, 44 species are recognized, distinguished using the morphological and anatomical characters



introduced by Barton (1901) and expanded by Hillis (1959); Hillis-Colinvaux (1980) also defined five distinct taxonomic Sections within the genus, based on anatomical details of the uncalcified nodes (see also “Internal structure” below).

Molecular systematics, first applied to the genus by Hillis et al. (1998) and expanded by Kooistra et al. (2002), yielded (i) a well-resolved phylogeny, (ii) confirmation of the five lineages, but requiring some re-organization, and (iii) demonstration of high cryptic species diversity, most tropical *Halimeda* species found consisting of two distantly related, genetic entities, which are indistinguishable by current methods of morpho-taxonomy. Verbruggen (2005) provides a detailed account of recent taxonomic progress within the genus.

### Distribution

*Halimeda* is a warm water alga well represented in the tropics, mainly on coral reefs. There is one species, *H. cuneata*, which is strictly subtropical, while a genetically distinct form of the tropical species *H. tuna* is the only species found in the temperate Mediterranean Sea.

Of the 30 species then recognized by Hillis Colinvaux in 1980, 77% occurred in the Indo-Pacific Region and 46% in the Western Atlantic Region (Caribbean). Of the 13 species in the Caribbean, seven also occurred in the Indo-Pacific. The remaining six endemic species are presumed to have evolved after the rise of the Isthmus of Panama closed the Central American Seaway, separating the Western Atlantic from the Pacific in the Miocene (circa 3.5 Ma ago).

On coral reefs, *Halimeda* can occur from protected lagoons to the shallowest reef flat environments, exposed seaward reef fronts and as deep as 140 m on fore reef slopes (Hillis-Colinvaux, 1985; Littler et al., 1986) (see also “Contribution to carbonate sediments” below).

While *Halimeda* is the only genus in the family *Halimedaceae*, it is closely related to the larger family *Udoteaceae*, which contains several other calcified, green macro algae, such as *Udotea*, *Penicillus*, and *Rhipocephalus*. These are often conspicuous in *Halimeda* habitats, as are several species of the closely related, but uncalcified, genus *Caulerpa* (family *Caulerpacaeae*).

### Internal structure

*Halimeda* segments consist of a central medulla of intertwining, branched, and sometimes anastomosing siphons (medullary filaments) running the length of the segment. These segments, with their large vacuoles, are continuous throughout the plant with a central few forming the uncalcified nodal region, a flexible joint between the segments. Within the nodes, the walls of the filaments may become thickened, fuse for part of their length, and even develop connecting pores, but there are no cross walls anywhere in the plant. The entire thallus is thus one multinucleate cell and is described as a **coenocyte**.

Near the segment surface, the medullary filaments branch vertically to form a cortex consisting of up to four layers of variously inflated utricles. The top layer (the primary utricles) is closely packed and appears polygonal in surface view. The size, shape, and branching patterns of these utricles are important taxonomic characters (Hillis-Colinvaux, 1980).

### Growth

Individual *Halimeda* thalli grow by producing new segments. These develop from small tufts of medullary filaments, which grow out from the distal perimeter of a segment at or near the tip of a branch. This process begins in the afternoon and the tuft of filaments becomes organized into a new soft, uncalcified segment overnight. This new segment is initially white, but by dawn it is bright green. A few hours after dawn it is whitish green, having already begun to calcify (see also “Diurnal color change (ii)” below). Fast growing branch tips can produce a new segment every few days.

### Calcification

The calcium carbonate endoskeleton is laid down in the internal spaces between the medullary filaments forming the segments. This is a light-driven process, requiring only that the superficial utricles contain functional chloroplasts and are closely adpressed, effectively isolating the interfilamental spaces from the external seawater. This happens within 36 h of initiation of the new segment.

Thereafter, whenever photosynthesis occurs, the resulting removal of CO<sub>2</sub> from the water in the interfilamental spaces raises its pH and causes deposition of calcium carbonate as aragonite crystals (Borowitzka and Larkum, 1976).

The overall degree of calcification varies (i) between species; (ii) within the algal thallus, with the lower, older segments more calcified than those at the growing tip; and (iii) with water depth and levels of irradiance.

### Diurnal color change

*Halimeda* thalli become almost white after dark and then green again by next morning. This is due to mass relocation of chloroplasts, and probably other organelles, from the peripheral utricles into the medullary filaments. There they remain, hidden beneath the calcium carbonate endoskeleton, until re-emergence begins a few hours before dawn. This mass relocation of organelles, which can only occur because of the coenocytic structure of the thalli, involves an extensive cytoskeleton of microtubules and actin fibers and will consume a considerable amount of energy every day (Drew and Abel, 1990; 1992). This energy-intensive endogenous rhythm may, however, give *Halimeda* crucial advantages in the dynamic coral reef environment, including

- (i) **Daily** – minimization of grazing damage because chloroplasts and other organelles are protected within the calcium carbonate endoskeleton when surface-scraping grazers are most likely to be active.

Rapid paling of the green segments also occurs in response to damage during the day.

- (ii) **Every few days** – relocation of chloroplasts beyond their parent segment allows the new segments, which develop overnight, to be populated with functional chloroplasts before dawn, via the nodal filaments. This allows calcification to start in the new segments at first light, rather than awaiting subsequent activation of its proto-chloroplasts by light-dependent *de novo* synthesis of chlorophyll.
- (iii) **Only once – immediately before death** – facilitation of rapid overnight redistribution of the entire contents of the medullary filaments into the superficial gametangia in preparation for holocarpic sexual reproduction (see also **Reproduction** below).

### Grazing

*Halimeda* is often found in abundance in areas on coral reefs where herbivorous fish exert high grazing pressure, but it is among the least preferred food items there. This is probably because of the high levels of calcification, a major physical defense against predation. In addition, the new segments, which are very vulnerable until calcified, are always produced at night when grazing pressure is low (Hay et al., 1988).

*Halimeda* also has chemical defenses against grazing. It synthesizes two secondary natural products, the diterpenoids halimetatetracetate and halimeditrial, which have considerable grazing deterrence properties, but are also potentially toxic to *Halimeda* itself. However, although both are present at high concentrations in the young, uncalcified segments, only reduced concentrations of the less toxic halimetatetracetate occur in the older segments, which are now heavily calcified, and so less vulnerable (Paul and Alstyne, 1988a).

Although these mechanisms can help to minimize grazing on *Halimeda*, it can still be heavily grazed, especially on seaward reef fronts where the lower parts of thalli, which have been severely cropped by herbivorous fishes are often found in inaccessible crevices. Once parts of a *Halimeda* thallus have been damaged, its coenocytic structure makes it vulnerable to catastrophic loss of cell contents. However, constrictions at branching points in the medullary filaments, and between the layers of cortical utricles, can quickly become plugged by organelles flowing toward the leak. This will retain the cell contents while the rapid wound repair processes temporarily seal the damaged area within a minute and construct a new wall within an hour (Menzel, 1988).

A very specific and widespread grazer on *Halimeda* is *Elysia halimedeae*, a small Saccoglossan Ophistobranch mollusc. It is a surface scraper completely undeterred by the diterpenoids, which help keep other grazers away. Instead, it actually modifies and accumulates the deterrent chemicals up to 7% of its body weight and then, when irritated, it secretes a defensive mucilage containing them (Paul and Alstyne, 1988b).

*Elysia halimedeae* is about 20 mm long and extremely cryptic as it is exactly the same color as the plants it feeds on. This is because it uses modified radula teeth to harvest intact chloroplasts from the outer utricles of *Halimeda* and stores them in specialized “digestive cells” within its body. This process is called **kleptoplasty**. The chloroplasts are unable to divide within the animal but can continue to photosynthesize and supply it with nutrition for weeks or even months (Trench, 1973; Evertsen et al., 2007). A number of other saccoglossan molluscs also use chloroplasts from other bryosidalean algae such as *Caulerpa* and *Codium*.

Another small animal closely associated with *Halimeda* is the crab *Huenia heraldica*, which grazes on the filamentous epiphytes growing on the segments. It is about 25 mm long, green in color, and has a wide, segment-like carapace. It does graze on *Halimeda* itself to a limited extent, removing segments, and holding them in small specialized claws on its upper body to complete its camouflage.

### Reproduction

*Halimeda* plants bearing gametangia were first reported by Derbes and Solier (1856) and Schmitz (1880). Both also reported the release of biflagellate zooids, although these were not demonstrated to be gametes until Nasr (1947) reported sexual fusion. However, collection of fertile plants has been so infrequent that Hillis Colinviaux (1980) still considered sexual reproduction to be of minor significance in the production of new *Halimeda* plants compared with asexual cloning involving rhizoidal runners and also the continued growth of dispersed plant fragments.

The paucity of field observations of sexual reproduction in *Halimeda*, even after the advent of scuba diving, is probably because it is completed in only 36 h. Healthy green plants transfer their entire protoplasm overnight into large numbers of newly formed, stalked bunches of gametangia that developed on the edges and surface of the segments the day before. The segments themselves are empty and white by dawn. These conspicuous green gametangia mature during that first day and explosively release their contents as gametes soon after dawn on the following day. This can produce a spectacular green soup of gametes in an aquarium tank, leaving a white thallus that is dead and soon disintegrates into a pile of calcified segments.

This process, whereby the plant dies after the whole thallus has taken part in simultaneous conversion of the entire cell contents to gametes, is called **holocarp**y.

Sexual reproduction in *Halimeda* is anisogamous and dioecious, two types of gametes being produced, each on different individuals. The larger “female” macro-gametes are bright green and contain a distinct red eyespot while the smaller ‘male’ microgametes are golden green and have no eyespot (Hillis-Colinviaux, 1980). Gametangia-bearing material is now known for most *Halimeda* species and gamete release and fusion have been reported upon in several, but development of zygotes has only been studied in the laboratory in one species, *H. tuna* from the

Mediterranean (Meinesz, 1980). Development was reportedly very slow and had not progressed beyond a small, uncalcified filamentous plant after 13 months. The characteristic *Halimeda* plant is presumed to be a haploid gametophyte, but it is not known when meiosis occurs, leading to speculation that a second, spore-producing, phase may be involved.

Some species of *Halimeda* may reproduce sexually at species-specific times of the year, while synchrony between field and laboratory populations, and also over considerable areas of *Halimeda* meadows, has been observed on the Great Barrier Reef (Drew and Abel, 1988b).

Recent observations show conclusively that sexual reproduction in seven species of *Halimeda* as well as 15 other Bryopsidalean algae from four genera, is an organized and pervasive phenomenon of coral reefs (Clifton and Clifton, 1999). It is comparable in synchrony and precision with the mass spawning of the corals themselves. Mass spawning of these green algae is also equally spectacular, releasing so many gametes that visibility on shallow reefs can be greatly reduced. Unlike the corals, however, in which entire populations spawn simultaneously on a single day, and live to spawn again next year, only a small part of the algal populations spawn each day, so that spawning can continue for several months, but the participating plants die and the population is progressively reduced. The lifespan of *Halimeda* thalli may be only months, to a maximum of a year, depending on species.

### Contribution to carbonate sediments

*Halimeda* segments may be shed intermittently by living plants or *in toto* after holocarpic sexual reproduction. They contribute much to the structure of coral reefs and atolls as they accumulate between the branching framework produced by the corals themselves. In some reefs, they also cascade down steep fore-reef slopes to form thick sediment deposits on the seabed (Freile et al., 1995).

In the outer lagoon of the Great Barrier Reef, *Halimeda* can also form extensive “meadows” between reefs, growing atop mounds of *Halimeda*-rich gravels, which have been deposited *in situ* by the meadows themselves (Drew and Abel, 1988a). The substratum, of loose dead segments, is stable enough to support *Halimeda* vegetation dominated by the same lithophytic species found on nearby coral reefs, rather than species with holdfasts better adapted to soft substrata. The individual mounds are typically 200–300 m in diameter, coalescing laterally to form 30 m thick banks several kilometers wide. These banks are easily identified by their sinusoidally undulating surface and characteristic seismic signature. They are usually associated with up-welling of cooler, nutrient-rich water from below the thermocline in adjacent oceanic waters (Wolanski et al., 1988), and have accumulated since the

underlying carbonate rock was exposed during the last low sea-level event 10,000 years ago. They have actually grown faster than the nearby coral reefs. Pinnacles of the underlying Pleistocene-age bedrock frequently occur in the hollows between the mounds of *Halimeda*-rich gravels (Phipps et al., 1985). Similar *Halimeda* banks have been found in Indonesian waters (Phipps and Roberts, 1988).

The banks closely resemble geological structures known as “bioherms” – dome-shaped structures composed mainly of the remains of one type of animal or plant (Marshall and Davies, 1988). Fossilized *Halimeda* bioherms are known from India, the Caribbean, and Spain. The latter form part of aerially exposed reefs and are described as “segment reefs.”

### Fossil Halimeda

The unlithified banks of *Halimeda*-rich gravels described above are potential precursors of the carbonate wackestones, rocks composed mainly of fossilized *Halimeda* segments, which occurred in fossil reefs as far back as the early Jurassic, circa 190 Ma ago. The carbonate structure is often very well defined and the rocks are relatively porous, due to voids between the loosely packed segments deposited *in situ*. There are also micro-voids within the segments reflecting the internal anatomy of the algae themselves.

These deposits are very similar to much earlier calcareous fossil algae (collectively known as Phylloid algae), which are widespread in ancient reefs in many parts of the world. Here, their considerable porosity has often allowed the accumulation of hydrocarbons (Wray, 1977).

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## Cross-references

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[Binding Organisms](#)  
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[Sediment Dynamics](#)  
[Sediments, Properties](#)  
[Tidal Jets](#)  
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## HALIMEDA BIOHERMS

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## Introduction

*Halimeda* Bioherms – two words with separate biological and geological connotations – have been used cojoined since 1985 by Davies and Marshall (1985) and Orme (1985) to describe Holocene mounds (bioherms) of dominantly *Halimeda* derived carbonates in water depths generally deeper than 30 m (sometimes 20 m) and forming undulating banks. Some confusion does exist within the literature, not because colleagues do not understand the use of the above authors but because of other discipline-related terms coined and used both before and since 1985. The geological understanding of Bioherm, therefore, needs to be clarified, as does its relations to a term coined at the same time – Biostrome – and their likely

(possible?) relation to the more recently coined biological term, Meadows. For these reasons, it is proposed to very briefly clarify as follows:

First, *Halimeda* are green calcareous precipitating algae from the phylum Chlorophyta in the order Bryopsidales and in two families – Halimedaceae and Udoteaceae. The taxonomy is described by Hillis-Colinvaux (1980) and in the Great Barrier Reef in various papers by Drew and Abel (see references in Drew and Abel, 1988a, b). There is no confusion over the term *Halimeda*, only sometimes over the identification of species.

Secondly, Bioherm is a geological term coined by Cummings (1932) to describe both bedded and nonbedded lens-like or mound-like accumulations, comprised of the often in situ accumulation of invertebrate organisms. The original definition had reefs in mind, invoking topographic relief above the sea floor, an in situ framework and rapid accumulation. In a modern sense, the bioherms described in this entry are not reefal, yet they are mound-like, often with significant relief above the surrounding sea floor and with internal characters, which are bedded or nonbedded and composed of in situ and derived biologic accumulations that have accreted rapidly. In a geological sense, mound-like structures sometimes show substantial mud and few framework organisms (many Carboniferous mounds) and are still legitimately termed bioherms. In the original definition, Cummings (op cit) distinguished bioherms from related structures termed Biostromes (see review by Kershaw, 1994), defined as nonreefal flat bedded structures often but not necessarily comprised of organic accumulations. It is noted here because Orme (1985) and Orme et al. (1978) rightly pointed out that in the northern Great Barrier Reef, large areas of the mid shelf behind the Ribbon Reefs (termed “back-reef” by Orme op cit) appear to be comprised of crudely bedded laterally extensive nonmounded “biostromal sediments” and are associated with *Halimeda* Bioherms (called “banks” by Orme et al., 1978). Later, Drew and Abel (1988a) described the surface characters of such areas as “Meadows” and Hillis-Colinvaux (1988), in a reef lagoonal environment, postulated that Meadows might evolve into Bioherms.

In the present contribution, *Halimeda* Bioherms are used to denote mounds showing relief above the surrounding sea floor and built by the in situ accumulation of *Halimeda* together with other infauna. They are sometimes called Banks (Orme and Salama, 1988) although Banks should rightly be reserved for much larger structures, for example, Bahama Banks. In the Great Barrier Reef and elsewhere, *Halimeda* Bioherms are associated with often larger areas having an extensive sheet-like form and called Biostromal areas (Orme and Salama, 1988, p. 136), the surface of such areas are called *Halimeda* Meadows by Drew and Abel (1988b). Thus, the origin of biostromes (a 3-D geologic term) might be elucidated by studying their surface “Meadows” (a 2-D biological term). Further, the origin of the Bioherms might be determined through studies of the spatially related Meadows/

**Halimeda Bioherms, Table 1** The species diversity of *Halimeda* meadows compared to adjacent reefs in the Great Barrier Reef region

| Species               | Meadows | Reefs   | Conclude                             |
|-----------------------|---------|---------|--------------------------------------|
| <i>H. opuntia</i>     | 0.6%    | 40.2%   | Reef dominant                        |
| <i>H. hederacea</i>   | 48.4%   | 38.3%   | Both reefs and meadows               |
| <i>H. copiosa</i>     | 26%     | 2.5%    | Meadows                              |
| <i>H. minima</i>      | Absent  | 0.2%    | In reefs at low level                |
| <i>H. micronesica</i> | 0.6%    | 10%     | Reefs                                |
| <i>H. distorta</i>    | 4.4%    | Absent  | Meadows                              |
| <i>M. melanesica</i>  | Absent  | 3.8%    | Reefs                                |
| <i>H. lucanalis</i>   | 0.5%    | 1.0%    | Both at low levels                   |
| <i>H. macrophysa</i>  | Absent  | 2.1%    | Reefs                                |
| <i>H. fragilis</i>    | 5.6%    | Trace   | Meadows                              |
| <i>H. tuna</i>        | 2.0%    | 1.0%    | Both at low levels                   |
| <i>H. discoidea</i>   | 1.1%    | 1.7%    | Both at low levels                   |
| <i>H. gigas</i>       | Absent  | 0.5%    | Reefs at low levels                  |
| <i>H. taenicola</i>   | 0.3%    | Absent  | Meadows at low levels                |
| <i>H. gracilis</i>    | 2.9%    | Absent  | Meadows                              |
| <i>H. incrassata</i>  | 7.2%    | Absent  | Meadows                              |
| <i>H. cylindracea</i> | 0.1%    | present | Meadows in trace amount              |
| <i>H. macroloba</i>   | trace   | present | Meadows and reefs at very low levels |

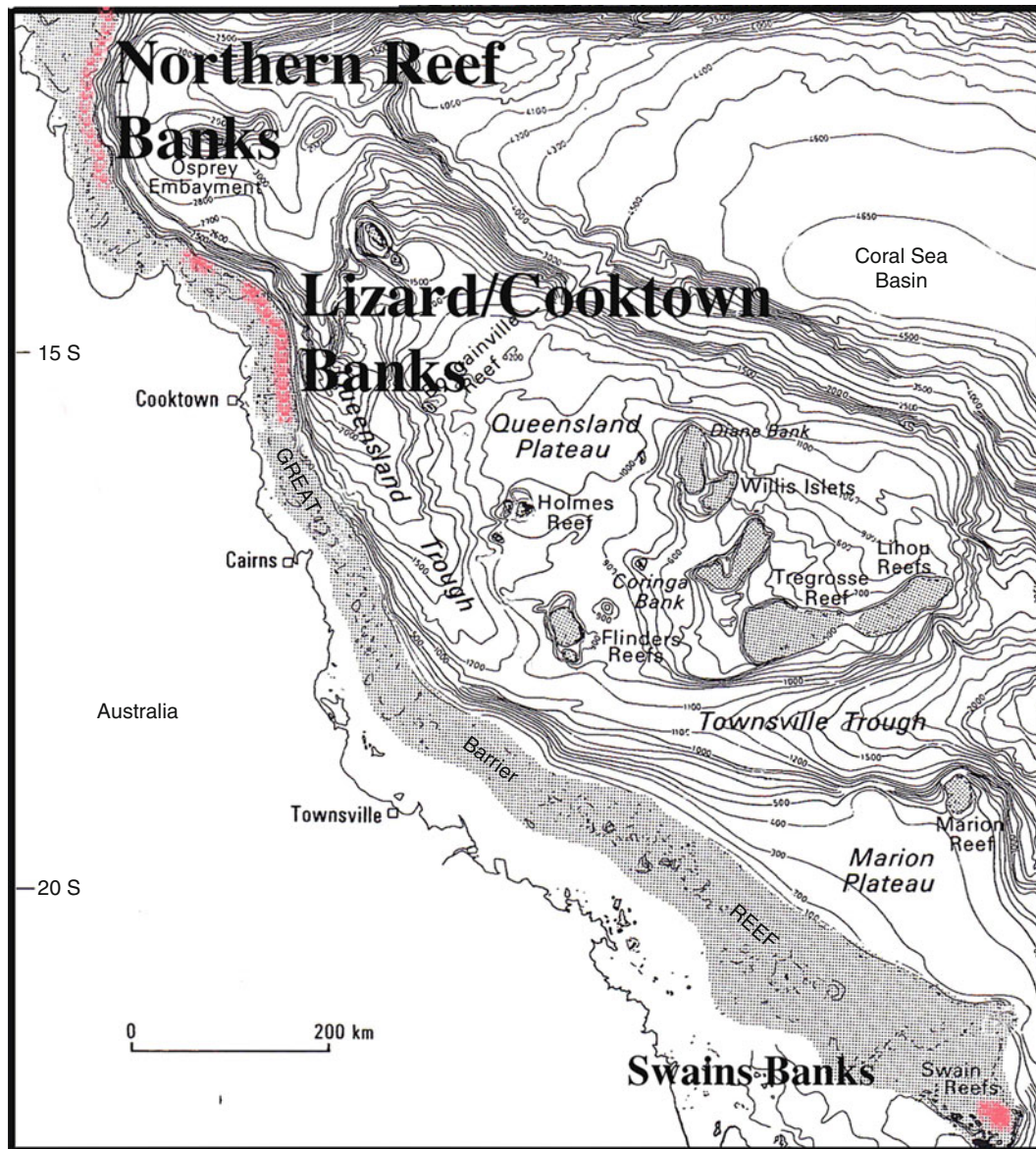
Biostromes. This entry follows this treatment. First however, the biology of *Halimeda* Bioherms and their related meadows are briefly reviewed.

### The biology of *Halimeda* bioherms and adjacent meadows (biostromes)

*Halimeda* are a green alga that belongs to the phylum Chlorophyta in the order Bryopsidales. *Halimeda* are described by Hillis-Colinvaux (1980, 1988) as being either Rhipsalian and possessing a holdfast or non-Rhipsalian and possessing none or a limited holdfast. In the modern environment, *Halimeda* occur as an accessory component of reefs, or as principal components of bioherms and meadows.

*Halimeda* Bioherms generally occur above a base line of 50 m water depth while meadows generally occur below this depth. The most extensive publications on their biology are those of Drew and Abel (1988a, b). The species composition of bioherms and meadows in the Great Barrier Reef is shown in Table 1.

Species diversity is high. A total of 12 *Halimeda* species, 2 *Udotea* and 1 *Penicillus* occur in water depths above 50 m dominated by the non-rhipsalian *H. opuntia* and *H. hederacea* while in water depths greater than 50 m, only *H. copiosa* and *H. hederacea* occur. Growth occurs via multiple obscure holdfasts restricted to the surface of the sediments. In other areas of the Pacific and Indian Oceans where *Halimeda* bioherms and meadows have been described, the same species predominate. Accumulations of *Halimeda* as meadows have also been reported from the lagoon of Enewetak atoll



**Halimeda Bioherms, Figure 1** Distribution of *Halimeda* bioherms in the Great Barrier Reef. They occur in three areas, Northern reef region, Lizard Island to Cooktown, and in the Swains reefs region.

(Hillis-Colinvaux, 1988) where the dominant species are the rhipsalian *H. incrassata* and *H. cylindrica*.

### The global distribution of *Halimeda* bioherms

#### The Great Barrier Reef

*Halimeda* Bioherms have been described in two areas: (1) two parts of the northern GBR and (2) in the Swains region of the southern GBR (Figure 1).

In the northern Region, *Halimeda* Bioherms have been described by two separate groups in the Lizard Island – Cape Flattery region and in the Ribbon 2–Ribbon 7 region.

The Lizard Island – Cape Flattery region (Figure 1) has been described by Orme and coworkers (Orme et al., 1978; Orme, 1985; Orme and Salama, 1988). They report that 26% of the total shelf area (effectively the outer shelf area behind the shelf edge reefs) between latitudes 14.27S and 15.02S is occupied by *Halimeda* litho-facies (Bioherms and Biostromal meadows). *Halimeda* bioherms are up to 19 m thick and sit on a prominent seismic reflector assumed to be the transgressed pre-Holocene/Pleistocene unconformity. The bioherms (= banks in Orme and Salama, 1988) that rise to within 25 m of current sea level are best developed in the eastern part of the region and their surface is mounded and “cloaked by *Halimeda* meadows – and



a limited veneer of reef coral – especially in troughs.” Little sedimentologic data on the *Halimeda* sediments and no dating have been published.

The bathymetry, seismic structure, submersible examination and photography, sedimentology, and biology of *Halimeda* banks in the region east of Cooktown (Figure 1) have been described by Davies and coworkers (Davies and Marshall, 1985; Phipps, Davies and Hopley, 1985; Marshall and Davies, 1988). They report that between 15.10S and 15.35S in the lee of Ribbons 2–7, the “reefless” tract supports a luxurious growth of *Halimeda* that during the Holocene have developed *Halimeda* bioherms in water depths between 30 and 50 m.

In the southern Great Barrier Reef region, *Halimeda* bioherms have been reported from the Swains reefs region, west of Frigate Shoals in water depths of 20–32 m (Figure 1) (Searle and Flood, 1988).

### The Sahul shelf

On the Sahul Shoals, *Halimeda* are integral components of large “banks” such as Big Bank, Snow White, Happy, Grumpy and Udang (Rees et al., 2007). The banks are generally flat topped with few bioherms in the sense of those described from the Great Barrier Reef.

### The Java Sea bioherms

In the Java Sea, Phipps and Roberts (1988) describe *Halimeda* bioherms on K Bank in the eastern part of the Makassar Straits (Figure 3). They are similar to those described from the Great Barrier Reef, if not a little larger.

### The Miskita bank/channel bioherms

Several generations of *Halimeda* bioherms occur on the shelf northeast of Nicaragua (Figure 4), as seen mainly on multichannel seismic sections.

### Descriptive features of *Halimeda* bioherms

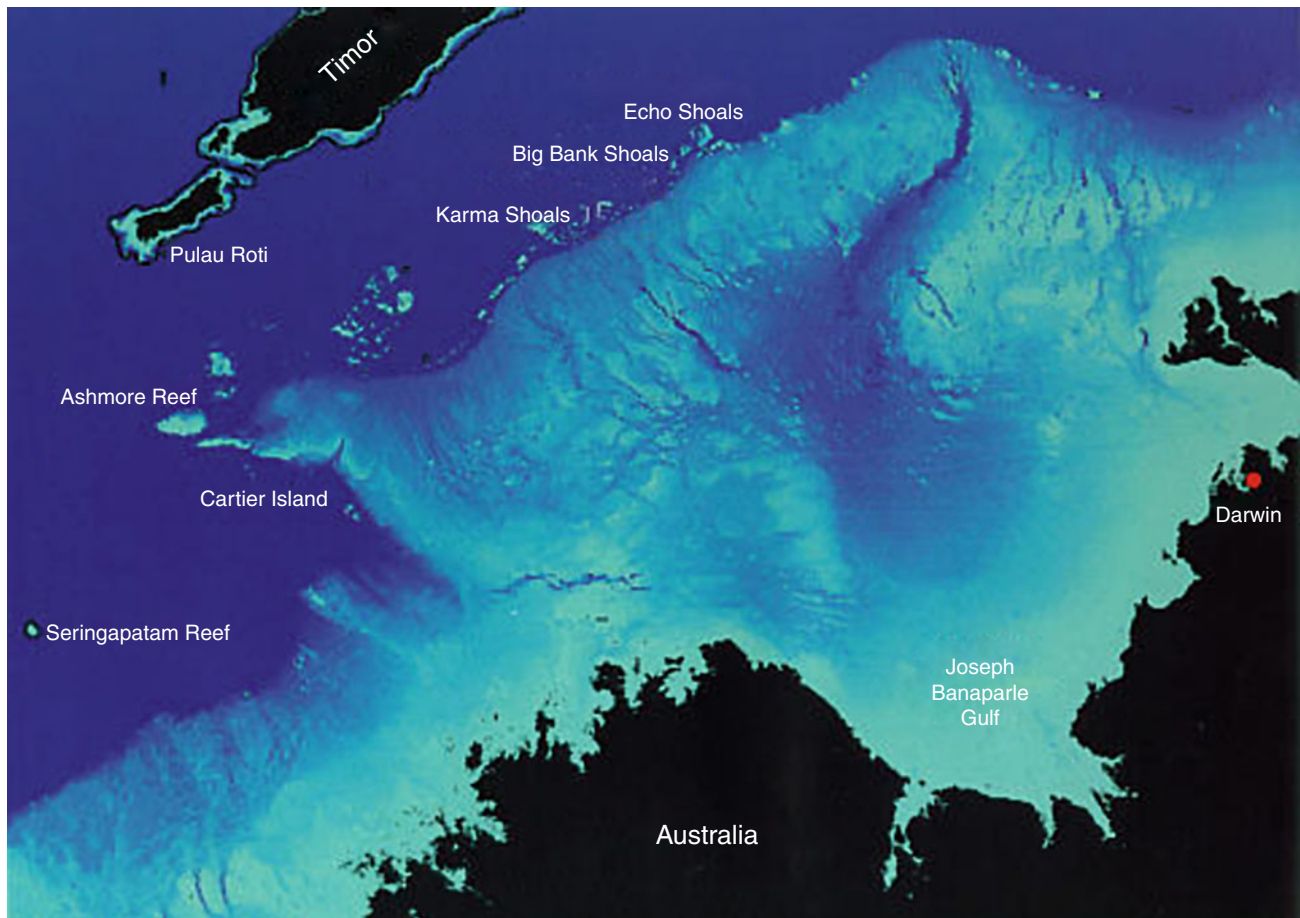
In the Great Barrier Reef, *Halimeda* bioherms occur over large areas behind the outer reefs, as “fields” or “complexes” of inter-fingering or inter-merging individual elongate bioherms, 150 m long (N–S) and 100 m wide (W–E), slightly flat topped and sloping away in all directions at 5–15° (Figure 5a). The most striking surface feature is a forest of soft green algae, sometimes 50 cm thick on the tops and thinning down the sides of each bioherm. This forest is dominated by various species of *Caulerpa* and *Halimeda*. Structurally, it is similar to rain forest in that there is a thick undergrowth on a sandy/gravelly surface, a middle layer of less dense cover and a top canopy. This forest is an ephemeral feature, appearing and disappearing within months. Mollusks, foraminifera, and bryozoans form integral and important parts of the epifauna with *Halimeda*. These collectively mantle the surface of the

top and sides of the bioherms but stop suddenly 3–5 m above the troughs between adjacent bioherms.

Seismic data shows in the Great Barrier Reef and the Java Sea, the bioherms are up to 15 m thick in the GBR (Figure 5a, b + c) but are substantially thicker (+20 m) in the Makassar examples (Figure 5d). In the northern Great Barrier Reef, the bioherms sit on a prominent seismic reflector (Figure 5a + c) which dips from around 33 m immediately west of the reefs to around 65 m some 5–10 km west of the reefs. The bioherms themselves also decrease in size and increase in depth in the same direction. The reflector in Figure 5a + c, is a leached skeletal, limestone whose vugs are partially filled with soil. The geometry of the bioherm complexes bear no relation to the geometry of the prominent reflector. A similar seismic reflector also underpins the bioherms in the Makassar Straits (Figure 5d).

Bedding is the commonest internal structural feature (Figure 5a–d); internally bioherms are sometimes bedded, sometimes transparent and often multigenerational. Individual bioherm complexes show bedding suggestive of several generations of growth. Tops are frequently seismically transparent. Sometimes, there are two seismic facies – a lower indistinctly bedded unit that merges laterally with a biostromal sheet facies and an upper bedded facies forming the upper two thirds of the banks.

Sedimentologically, as seen in cores (Figure 6), the bioherms are comprised of *Halimeda* sands and gravels in an olive green matrix. Large foraminifera, *Marginopora vertebralis* and *Alveolinella quoyi* are subordinate but important parts of the gravel fraction, as are mollusks and bryozoans. The *Halimeda* are dominantly *H. opuntia*, *v. hederacea*, and *H. copiosa* with subordinate amounts of *H. fragilis*, *H. discoidea*, and *H. gracilis*. Texturally the bioherms are gravelly, sandy muds throughout but with slight textural variations down the core. At the surface, the gravel fraction (largely *Halimeda*) comprises 50%, this dropping to 20–30% within 1 m of the top. Deeper in the core the gravel fraction either remains at 20–30% or drops even further to less than 10%. The sand fraction in most cores stands at 20–30% and is comprised dominantly of broken *Halimeda* leaves with contributions also from foraminifera, bryozoans, and mollusks. Mud in the cores measures around 10% in the top half meter of the cores and then increases substantially to between 30 and 50% throughout the rest of the core. Approximately half of this mud fraction is carbonate and half non-carbonate or terrigenous (quartz, kaolinite, and smectite). However, in the Swains Reefs bioherms, the mud matrix is totally carbonate and devoid of terrigenous material, reflecting the distance of these bioherms from the Australian mainland. In the Java Sea, Phipps and Roberts (1988) describe the bioherms as disarticulated *Halimeda* plates with a fine grained matrix of foram-rich carbonate mud (usually less than 40%), only a small percentage of which is non-carbonate (volcanic shards and siliceous spicules). In some cores, *Halimeda* plates form a disorientated open-textured accumulation. Locally, within cores, sediments



**Halimeda Bioherms, Figure 2** *Halimeda* bioherms in the region of the Sahul Shoals, Timor Sea.

are composed of coarse *Halimeda* plates, some of which are still unbroken. Occasionally, layers 5–10 mm thick are comprised of *Halimeda* plates orientated parallel to the bioherm surface.

#### Rates of growth of *Halimeda* bioherms

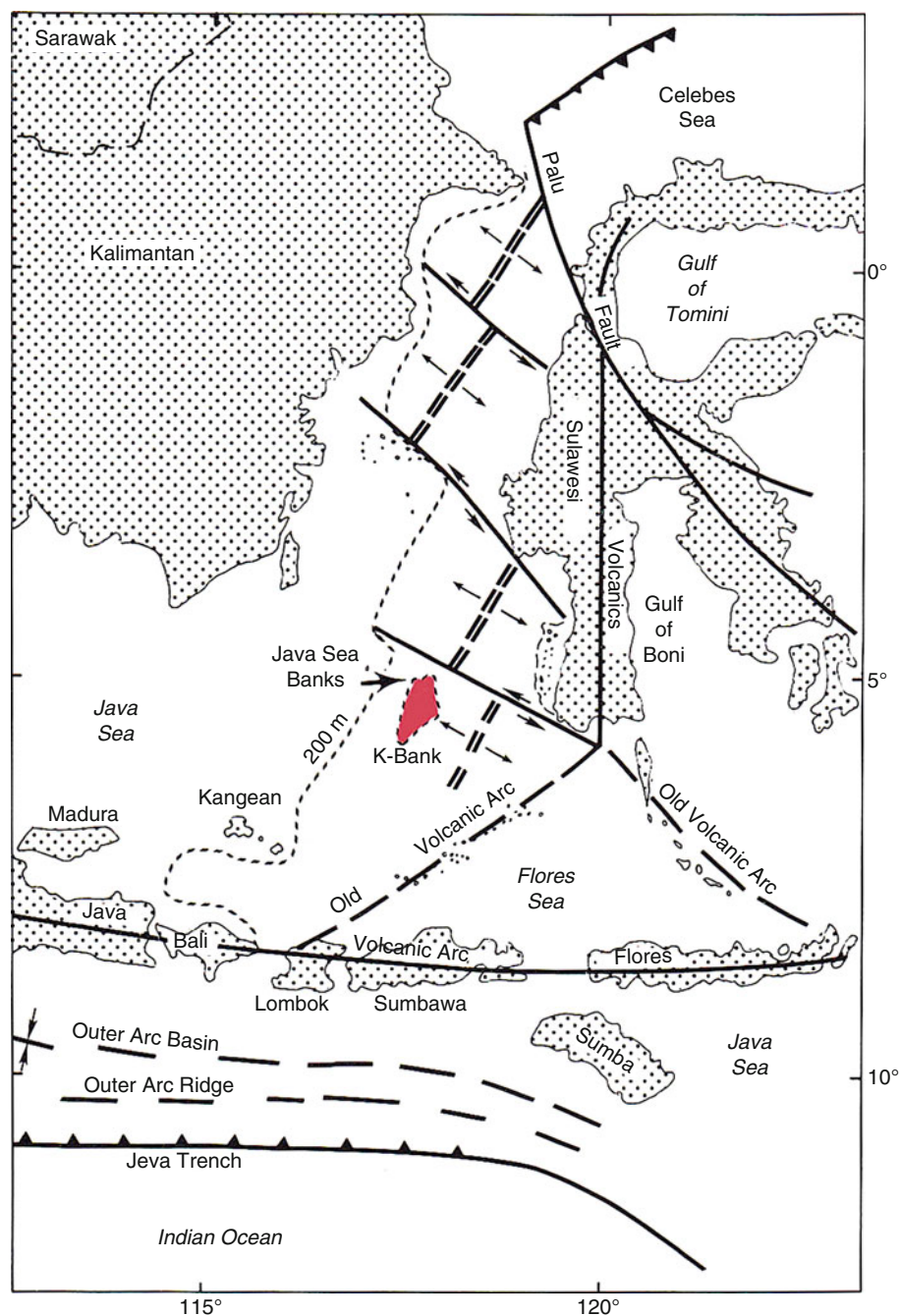
Biologic studies report a wide range of growth rates for *Halimeda*, varying from  $420 \text{ g CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$  in the Florida Straits to  $2,234\text{--}3,000 \text{ g m}^{-2} \text{ year}^{-1}$  in the Great Barrier Reef (Drew, 1986). The high rates in the GBR are attained by the plant doubling the biomass of the colony every 15 days. This represents an enormous production of carbonate sediments indicating that *Halimeda* are a major contributor to tropical marine environments. The bioherms described in this entry are testimony to that conclusion. Radiocarbon dating (Table 2) provides some indication of the vertical accumulation rates of the bioherms in the Great Barrier Reef and Makassar Straits.

Table 2 indicates clearly that accumulation rates have been similar in both the Great Barrier Reef and in the Makassar Straits. Depending on porosity, accumulation

rates of close to 3 m/1,000 years are very close to Drew's estimates and confirm that not only are *Halimeda* significant contributors to reef ecosystems, but that they are capable of producing geologically significant ecosystems in their own right.

#### Relations between bioherms (banks) and meadows (biostromes) and the lagoonal meadows at Enewetak

In the Great Barrier Reef, Bioherms are intimately associated with widespread crudely bedded areas which are not mounded and which have been described by Drew and Abel (1988a) as Meadows. Such areas occupy a range of water depths but often deeper than 50 m and extending down to 96 m in places. Similar deposits are reported to occur extensively over K bank east of Makassar Straits. The growth of such features and their relations to the truly biohermal deposits is, therefore, pertinent to the current discussion. Clues as to growth were defined at Enewetak by Hillis-Colinvaux (1988) where various ages of thalli (successional development) were observed to spread

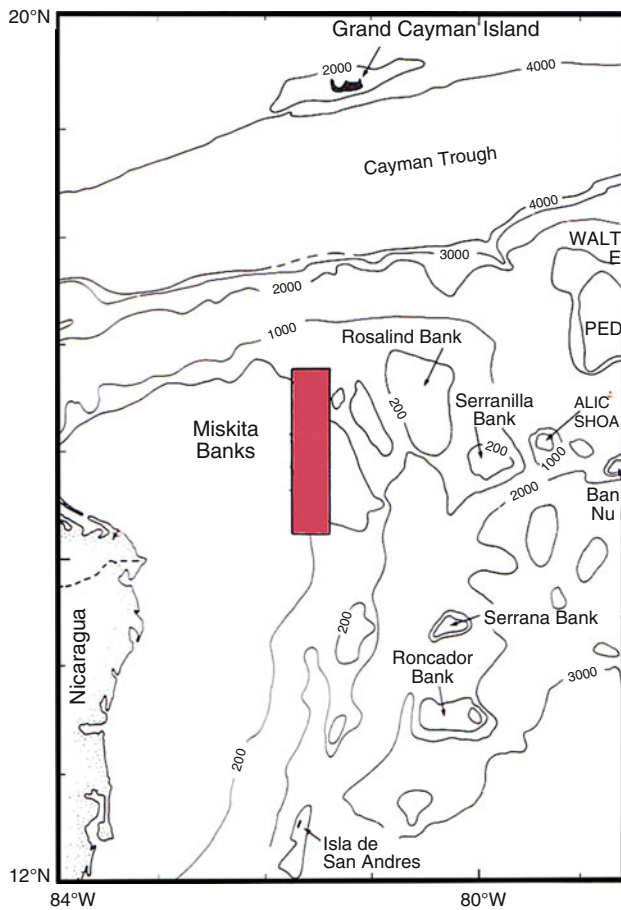


**Halimeda Bioherms, Figure 3** *Halimeda* bioherms in the Java Sea, in the region of the Macassar Strait (After Phipps and Roberts, 1988).

across unconsolidated sediment producing a raised terrace above neighboring barren sands. First, an extensive holdfast system developed together with buried thalli; secondly, *Halimeda* plates were shed and they and associated sediments were stabilized by cyanobacterial

algal mats; thirdly, elevation of thalli above the sediment surface anchored by the holdfast system with further in situ accumulation of plates and platelets and further stabilization by mats; fourthly, the development of an associated flora and fauna, particularly sponges and fifthly,





**Halimeda Bioherms, Figure 4** *Halimeda* bioherms on the Nicaraguan shelf in the region of the Miskita Channel (After Hine et al., 1988).

a thickness was achieved by continuous shedding from perennial growth and algal mat development. This may define a mechanism of growth applicable to the early stages of meadow development of the transgressed Pleistocene surface. However, Drew and Abel (1988a) showed that shallow meadows in the Great Barrier Reef are comprised of non-Rhipsalian algae without strong holdfasts. Further work is required to determine whether such meadows grow out of meadows like those at Enewetak.

### Growth of *Halimeda* bioherms

A number of features are pertinent to growth and origin:

1. They grow from a prominent surface defined in the Great Barrier Reef as the transgressed Pleistocene surface. A similar reflector also occurs below the Makassar Strait bioherms and is also interpreted as the Pleistocene transgressed surface. The shape of biohermal mounds bears no relation to any minor relief

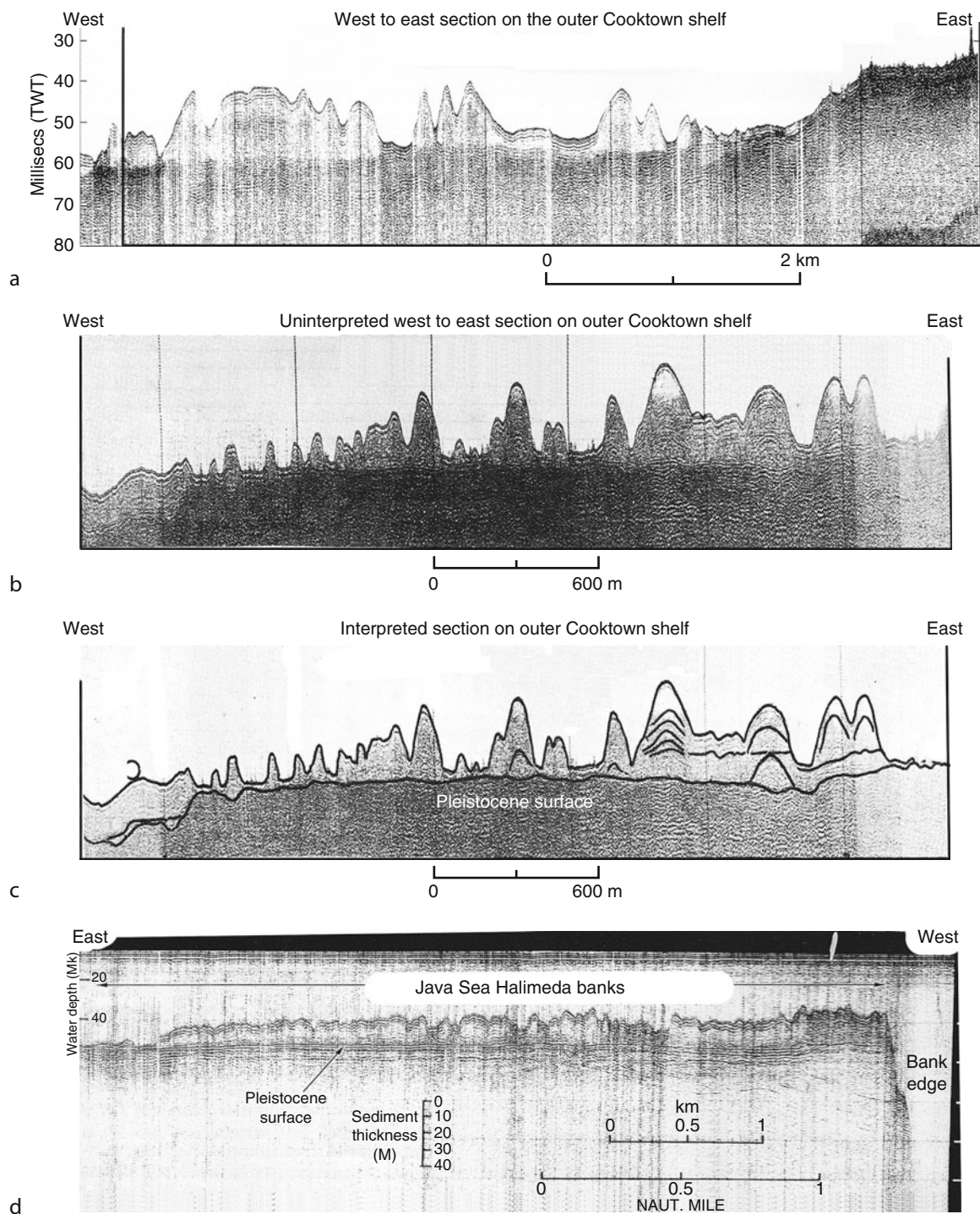
features on this transgressed surface. There is little antecedence effect.

2. They occur intimately associated with sheet-like bedded biostromal deposits (Meadows).
3. In the Great Barrier Reef they occur in the lee-shelter of the Holocene outer barrier.
4. At least in the Cooktown region, they are largest close to the outer barrier, becoming smaller to the west.
5. They are comprised of in situ and derived accumulations of *Halimeda* leaves and an associated fauna of foraminifers, bryozoans, and mollusks, which form a series of multigenerational mounds, sometimes bedded, sometimes transparent.
6. In the Great Barrier Reef and in the Makassar Strait, their presence on the same Pleistocene surface that underlies the modern reefs, places their age as post Pleistocene, growing at the same time as the Reefs. Radiocarbon dating corroborates this conclusion.

The relations (if any) of Bioherms to the Biostromal meadows has intrigued many. Orme et al. (1985, 1988) and Davies and co-workers (1985, 1988) have drawn attention to the co-occurrence of bioherms and biostromes (meadows) and Davies and coworkers in particular cite a variety of evidence (seismic, bathymetric, and visual observations from submersible) to indicate that meadows grade into biohermal areas. In the Great Barrier Reef, a case can be made, therefore, to suggest that meadows (biostromes) first occupied the transgressed Pleistocene surface and evolved into bioherms in places favorable to vertical growth. However, the development of a vertical growth potential demands special conditions and Davies et al. (op cit) and Drew and Abel (1988b) point to the likely importance of enhanced nutrients as an essential requirement. Thompson and Wolanski (1984) proposed that strong tidal currents operating in the inter-reef channels produce a Bernoulli Effect, lifting off-reef water onto the shelf through passes deeper than 50 m. Further Wolanski et al. (1988) propose that off the Cooktown region, upwelling and development of a tidal jet is occurring and carrying nutrient rich water from a reef passage to the *Halimeda* meadows. Such upwelling is limited to channels shallower than 45 m. These mechanisms add substantial weight to the timing and modes of origin defined by Davies and Marshall (1985) and summarized in Figure 7.

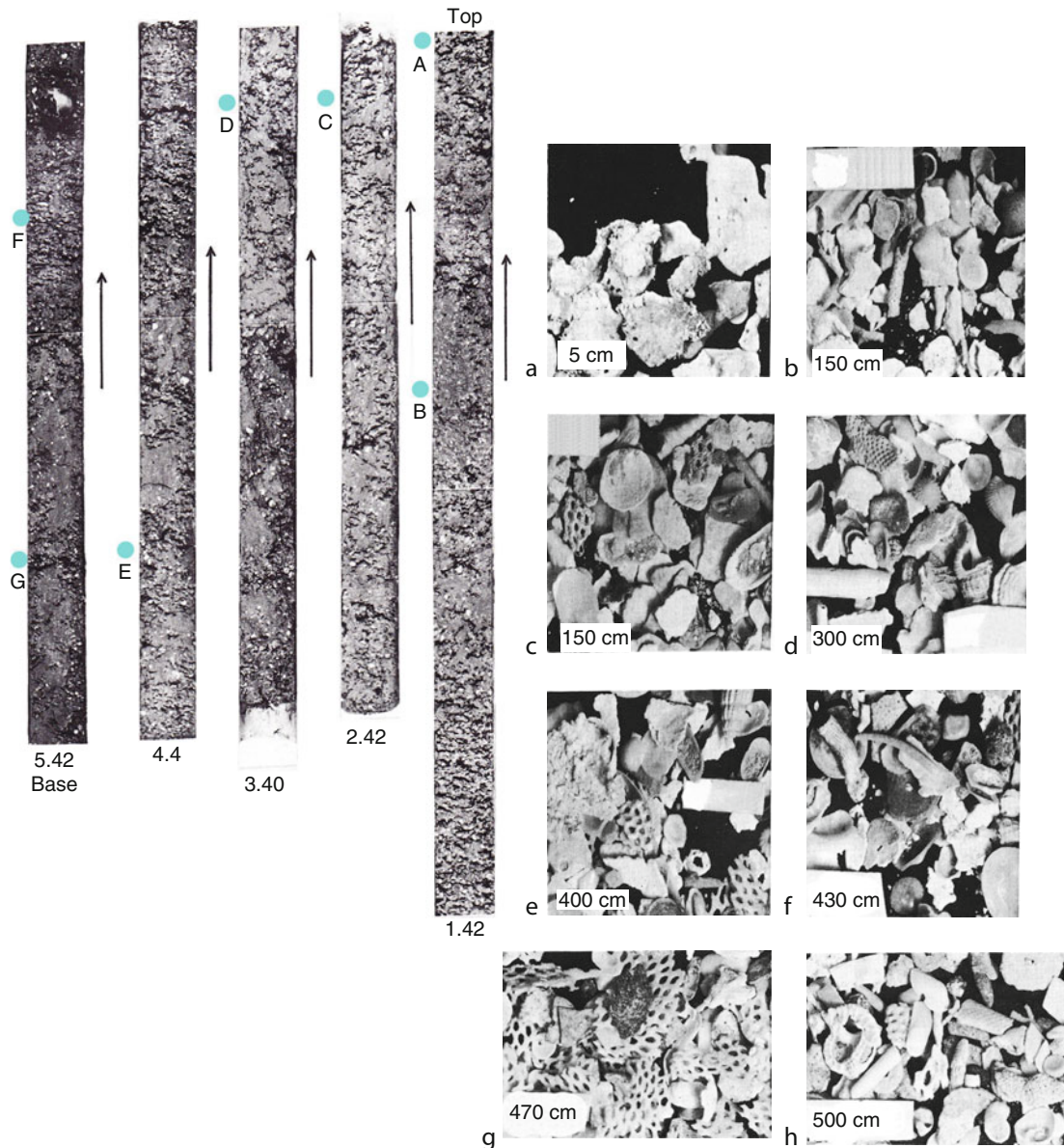
### Significance of *Halimeda* bioherms

Originally the term "bioherm" was coined and used by petroleum geologists, particularly in an exploration sense, to describe features that did or could contain petroleum. Thereafter, it became synonymous with "reef-like" structures and important targets in petroleum exploration. Davies et al. (1988) described *Halimeda* bioherms as potential exploration targets in the Australian region. More recently, however, Davies and Marshall (1985) pointed out a different and perhaps more significant



**Halimeda Bioherms, Figure 5** (a) West to east seismic section across the outer Cooktown shelf showing bedded nature of the *Halimeda* banks in 30 m of water. (b + c) Uninterpreted and interpreted seismic section across the banks on the outer Cooktown shelf. The multigenerational nature of the banks together with their planar Pleistocene growth surface clearly visible. (d) Seismic section of thick *Halimeda* banks in the Makassar Strait, Java Sea. The banks are clearly sitting on a planar surface interpreted as the Pleistocene.





**Halimeda Bioherms, Figure 6** Cores from the *Halimeda* banks on the Cooktown shelf. The positions of detailed photographs are shown on the cores.

feature of *Halimeda* bioherms in the Great Barrier Reef at least, that is, they produce  $3 \text{ kg CaCO}_3 \text{ m}^2 \text{ year}^{-1}$  compared to 3–4 kg for the reefs; however, the bioherms occupy a larger area. They may, therefore, lock up a greater proportion of  $\text{CaCO}_3$  than do the reefs. Since the correlation between carbon dioxide ( $\text{CO}_2$ ) levels and global temperatures was established in the ice core records, this conclusion assumes an even greater significance because it indicates not only the relevance of calcareous algae as important additional  $\text{CO}_2$  sinks but when

estimated on a global basis it also doubles the contribution of shallow water carbonate sediments (in conjunction with reefs) as  $\text{CO}_2$  reservoirs (Rees et al., 2007).

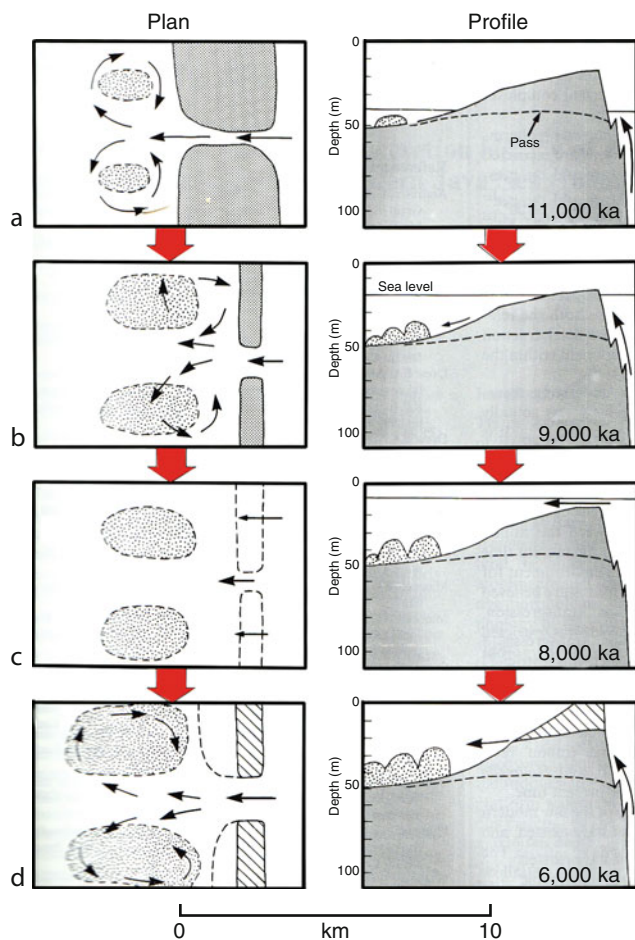
### Summary

*Halimeda* bioherms have been described from three parts of the Great Barrier Reef: from the Sahul Shelf, from the Makassar Straits, and from the Nicaraguan Bank. They form mounds that are up to 20 m height and are comprised of the skeletal remains of various species of *Halimeda*



**Halimeda Bioherms, Table 2** Vertical accumulation rates of bioherms in the Great Barrier Reef and Makassar Straits

| Region   | Location   | Exact position | Ages (years BP) | Sed rate           |
|----------|------------|----------------|-----------------|--------------------|
| GBR      | North bank | 0–5 m          | 270–2,760       | 2 m/1,000 years    |
| GBR      | Big bank   | 0.4–2.8 m      | 270–1,300       | 2.33 m/1,000 years |
| GBR      | Big bank   | 2.8–5.4 m      | 1,300–4,750     | 0.75 m/1,000 years |
| Java Sea | PC 12      | 0–100 cm       | 0–1,000         | 1 m/1,000 years    |
| Java Sea | PC12       | 100–250 cm     | 1,000–1,250     | 0.6 m/1,000 years  |
| Java Sea | VC 4       | 0–250 cm       | 0–1,250         | 0.2 m/1,000 years  |
| Java Sea | VC 4       | 250–450 cm     | 1,250–2,000     | 2.7 m/1,000 year   |



**Halimeda Bioherms, Figure 7** Origin of *Halimeda* bioherms as proposed by Davies and Marshall (1985). The key to growth are strong nutrient eddies produced by jets of upwelled oceanic waters flooding through the inter-reef passes before the modern reefs began in the time frame 11–9,000 ka (a + b). *Halimeda* banks grew well in this time frame. However, when the Pleistocene substrate was topped by the rising sea level (c) nutrient concentrations were not delivered specifically to the banks but, generally, to the leeward environments. Bank growth may have slowed down at this point. However, when the Holocene reefs reached sea level, flow into the back reef was again forced through the passes, leading to more nutrient availability and a spurt in the growth of more banks (d). Thus multigenerational growth relates to nutrient flux.

(*H. opuntia*, *v. hederacea*, and *H. copiosa* with subordinate amounts of *H. fragilis*, *H. discoidea*, and *H. gracilis*) together with large benthic foraminifera, mollusks, and bryozoans. The bioherms are bedded, sometimes transparent and often multigenerational, and sit astride the late Pleistocene transgressed surface. They have grown at the same time as the adjacent reef ecosystem and at rates almost equivalent to the reef systems. This suggests not only a critical relevance of calcareous algae as important additional CO<sub>2</sub> sinks but when estimated on a global basis it also doubles the contribution of shallow water sediments (in conjunction with reefs) as CO<sub>2</sub> reservoirs.

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## Cross-references

[Bioherms and Biostromes](#)  
[Great Barrier Reef: Origin, Evolution, and Modern Development](#)  
[Halimeda](#)  
[Solution Unconformities](#)

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## HAWAIIAN EMPEROR VOLCANIC CHAIN AND CORAL REEF HISTORY

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### Definition

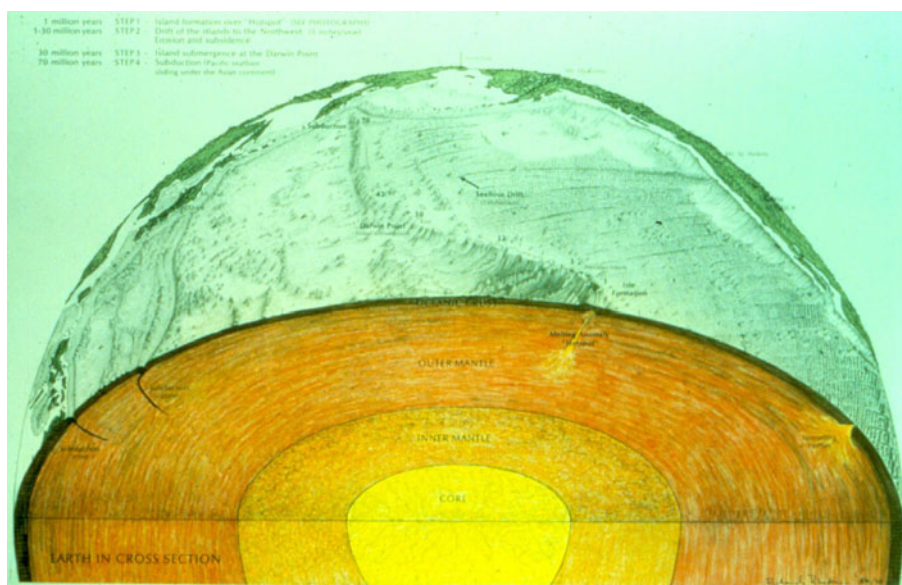
The palaeoceanography of the Hawaiian Emperor volcanic chain of islands and seamounts and the presence of coral reefs share an incomplete history. The first known Hawaiian Island to emerge from the Hawaiian hotspot was Meiji Guyot approximately 70+ Ma ago. Today, movement of the Pacific Plate has transported Meiji Guyot from its original location at approximately 19° north latitude and 157 west longitude almost 6,000 km to the northwest to about 54° north latitude, to a location near the edge of the juncture of the Kuril and Aleutian trenches, virtually on the edge of subduction below the Asian Plate (Figure 1). Unlike all of the islands in the Hawaiian Archipelago today, Meiji Guyot was never surrounded by a coral reef. Present theory, if correct, holds that the first half of the Hawaiian Emperor history was devoid of coral reefs (Grigg, 1988). Several explanations have been advanced to explain their apparent absence during this early period of Hawaiian history.

However, before discussing the palaeoceanographic evidence for the early absence of coral reefs in Hawaii, it

is first important to reiterate the chronological, geographic, and geochemical evidence that shows that all of the Emperor Seamounts and Hawaiian Islands in the chain originated from the same hotspot in the North Pacific (Wilson, 1963; Morgan, 1972). Perhaps the best evidence for a common origin of the volcanoes over the Hawaiian hotspot is the continuous age progression (K-Ar radiometric dates) of the volcanic edifices with distance from Kilauea (location of the present hotspot) (Jackson et al., 1980, Figure 4). Relatively continuous motion of the Pacific Plate at about 8 cm/yr over the Hawaiian hotspot during the last 70+ Ma resulted in the formation of an almost linear geographic chain of volcanic islands. A bend in the chain at approximately 43–50 Ma is explained by a shift in the direction of plate propagation from north to northwest. The geo-chemical evidence for Hawaiian volcanoes and the Emperor Seamounts also supports the common origin hypothesis. All the lavas exhibit a similar sequence of eruption (tholeiitic followed by alkalic basalts) as well as similarities in chemical composition of all the basalts (Fletcher et al., 2008; Rooney et al., 2008).

The claim that coral reefs were absent in the Hawaiian chain during the first half of the Tertiary rests on the fossil record of shallow marine organisms in the Hawaiian Emperor (H-E) Chain today. The oldest reef corals that have been recovered from dredged limestones and deep-sea drilling cores in the Emperor Seamounts and guyots, range between 21 and 34 Ma. The oldest samples (33 and 34 Ma) are specimens of *Porites* and *Astreopora* from Kanmu and Yuryaku Seamounts (Grigg, 1988). The biostratigraphy based on cores from the older and more northern Emperor Seamounts (Ojin, Nintoku, Suiko, and Meiji) consists primarily of a tropical biofacies of shallow warm water coralline algae, bryozoa, benthic foraminifera, ostracods, spirorbids, echinoid spines, bivalves, and brachiopods, but no reef building corals (Jackson et al., 1980). Possible causal factors for their absence could be sampling error, a more northerly position of the palaeo-Hawaiian hotspot, cooler sea-surface temperatures in the Paleogene, rarity of corals worldwide in the early Tertiary, or insufficient transport of coral larvae from the Indo-West-Pacific (IWP). While a combination of these factors could also explain the early absence of coral reefs in the history of the H-E chain, the theory that is best supported by the palaeoceanographic history of the Pacific Ocean, is isolation of the Hawaiian Archipelago from the IWP (Grigg, 1988). All of the fossil corals and all of the reef corals that exist in the H-E chain today are IWP in origin, although some endemism (~25%) has evolved over time.

During the middle Tertiary, a series of gradual palaeoceanographic changes, including closure of the Tethys Sea, development of thermohaline circulation, isolation of Antarctica, and intensification of latitudinal temperature gradients are believed to have combined to intensify gyral circulation in the North Pacific Ocean (Kennett, 1982). As a result, the Kuroshio Current in the Western Pacific and the Subtropical Counter Current would have



**Hawaiian Emperor Volcanic Chain and Coral Reef History, Figure 1** Cutaway of the earth showing the location of the Hawaiian hotspot and the Hawaiian-Emperor chain of islands and seamounts from Hawaii in the southeast to Meiji Guyot at the juncture of the Kuril and Kamchatka trench subduction zone.

strengthened and both are sources of transport of IWP coral larvae into the northern Pacific Ocean. Hence, the sudden appearance of reef corals in the Hawaiian Archipelago and their continual presence throughout the Neogene to the present day might best be attributed to ocean circulation. Even today, the coral fauna of Hawaii is highly attenuated and consists of less than 10% of the coral species now present in the IWP.

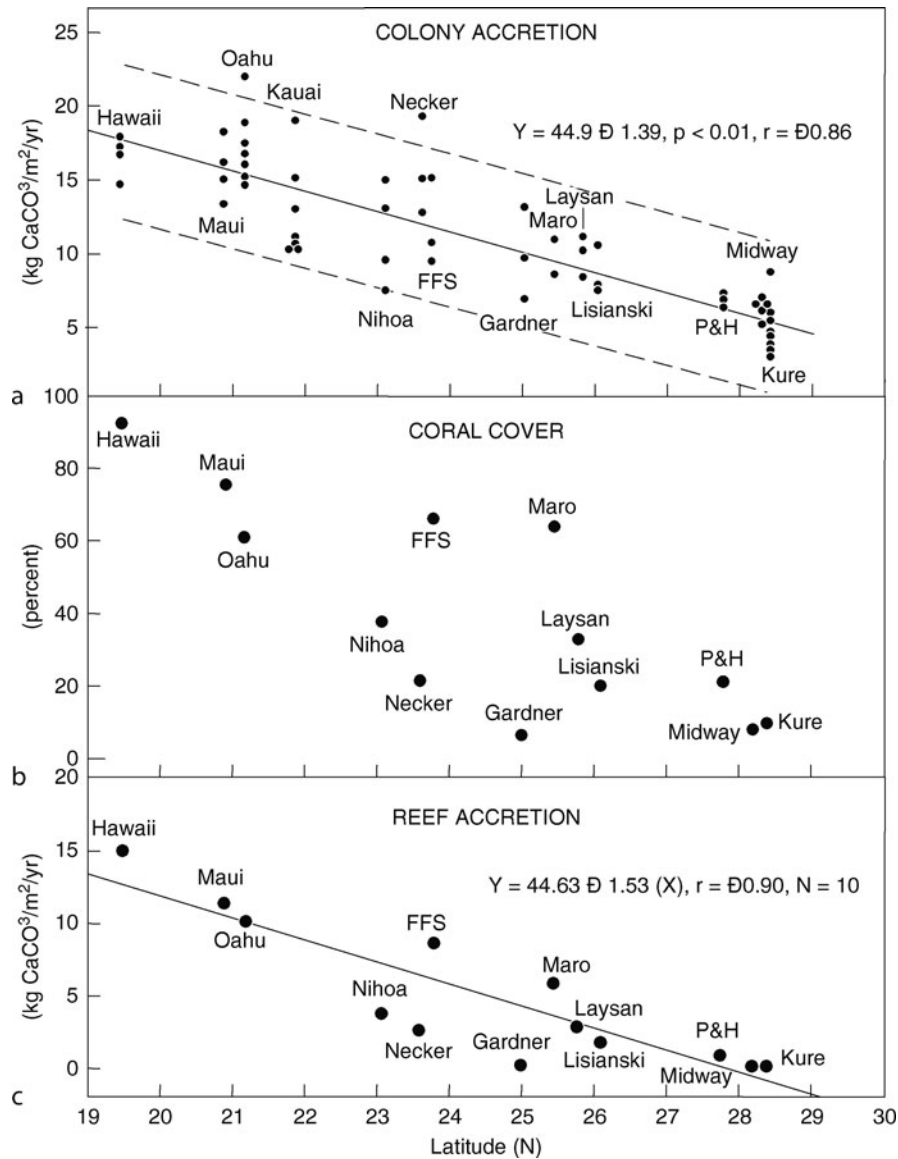
Although the fossil record shows that reef corals have been in the Hawaiian Archipelago since Mid-Oligocene time, a moderate degree of taxonomic turnover has occurred. Extinction and re-colonization events are particularly evident in the Midway core from the present all the way back to early Miocene time (Wells, 1982). This is not surprising, nor unexpected, given the northerly position of the Hawaiian Islands near the latitudinal limits of reef building corals as well as their relative isolation from island stepping stones to the south and west.

Today, approximately 59 species of reef building corals have been recognized in the main Hawaiian Islands while 57 are reported in the Northwestern Hawaiian Islands (NWHI), (Maragos et al., 2004). These totals, while significant, are still relatively depauperate compared to the IWP where about 700 species are reported to exist (Veron, 2000). The low species diversity of modern Hawaiian reef building corals underlines the significance of the isolation of the Hawaiian Archipelago, as well as, its northerly latitude. The effect of latitude is particularly important when applied to the growth rate of individual corals.

Using *Porites lobata* as a proxy for all other common reef corals in the Hawaiian Archipelago, Grigg (1982, 1997, 2008) showed that growth rates at the southeastern end of the chain are typical of tropical coral growth rates in general, while moving northwest in the chain, they decline in a linear fashion almost as a direct function of latitude (Figures 2 and 3). At the very end of the Archipelago, at a latitude of  $\sim 29^\circ$  north at Kure Atoll, the net growth rate was found to be virtually zero if losses due to bio-erosion, mechanical erosion, and the subsidence rate of the island were all taken into account. If this fact is considered over geological time in combination with the northwesterly movement of the Pacific Plate, then subsequent drift of the atoll to the northwest would cause it to gradually drown, setting the northern limit (threshold) of atoll formation (Grigg, 1982). In recognition of Darwin's original theory of atoll formation (Darwin, 1842), Grigg labeled this threshold "The Darwin Point".

Looking at coral reefs today in the Hawaiian Archipelago, they span about  $10^\circ$  of latitude stretching from optimal environments in the southeast to those in the northwest at the extreme limits of coral reef growth. Considering the natural constraints associated with this geography, most Hawaiian reefs today are exceptionally healthy. The most common natural disturbance events are large episodic waves that abrade and scour the reefs (Dollar, 1982). Within the major high Hawaiian Islands from Hawaii to Kauai, the most significant anthropogenic impacts include sedimentation events from land runoff,



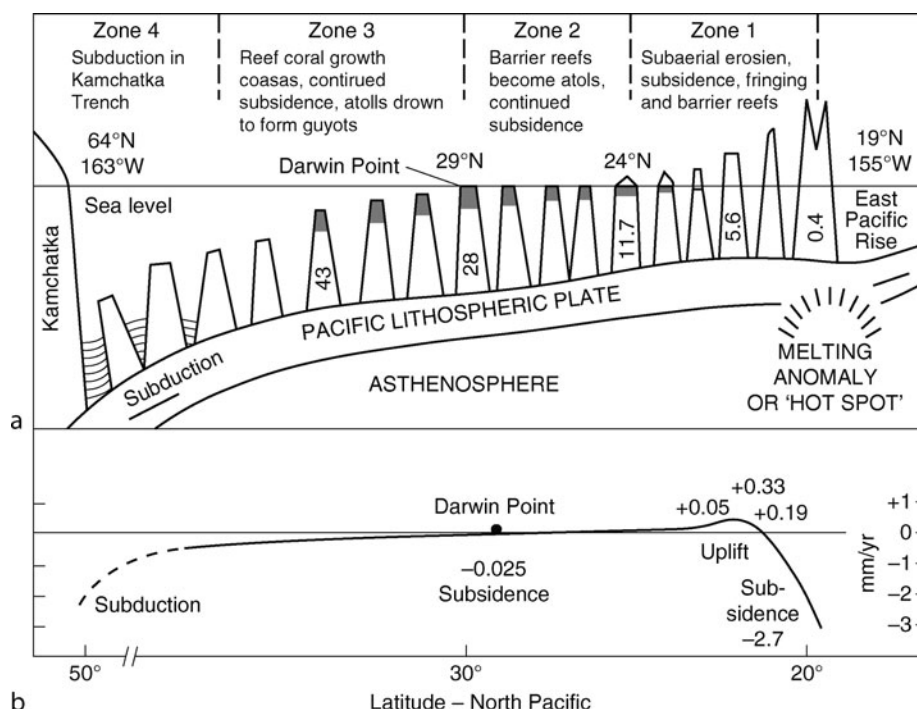


**Hawaiian Emperor Volcanic Chain and Coral Reef History, Figure 2** Colony accretion of *Porites lobata*, coral cover, and reef accretion on seaward reefs off all major Hawaiian Islands. Note that coral reef accretion goes to zero near 29° north latitude.

eutrophication in areas of confined circulation, particularly in shallow water bays and on reef flats, and widespread over-fishing of reef fish on practically all offshore reefs. There is an urgent need to strengthen the enforcement of fish and game regulations by the State of Hawaii. The State should also actively increase the number of Marine Protected Areas (MPA's) in the main islands where today only about 1% of the coastline is protected. In contrast, the NWHI have been almost completely protected under a recent (2006) Executive Order that reclassified the entire area (except Midway Island) as a Marine Monument.

## Outlook

Looking ahead toward the present century, particularly with regard to global climate change (GCC), coral reefs in the Hawaiian Archipelago may be relatively well situated. The four most important factors associated with GCC that may affect coral reefs are sea-level rise, increases in sea surface temperature, increases in ocean acidification, and increased storminess. Rising sea level may pose a flooding problem for the lowest isles in the northwest but it will also raise the "lid" providing more accommodation space for coral reef growth to take place on most island shelves throughout the chain. Given the northern latitude of



**Hawaiian Emperor Volcanic Chain and Coral Reef History, Figure 3** Schematic figure of the Hawaiian-Emperor chain showing Zones 1–4 tracing the evolution, subsidence, drowning, and subduction of volcanic edifices and the location of the Darwin Point and northern limit of drowned guyots (From Scott and Rotondo, 1983).

the Archipelago, rising sea surface temperature may not be as great a problem as it could be for more tropical reefs. Although effects due to increasing ocean acidification are not well understood, large carbonate deposits that exist throughout the Archipelago may buffer the potential impacts of slightly lower pH. Increased storminess is also hard to predict depending on frequency, magnitude, and location, but if larger wave events are produced, then intermediate disturbance may become more limiting to coral development and abundance. Overall, while it may be premature to predict dire consequences for the health of coral reefs globally, the coming century clearly contains as many challenges as it does uncertainties.

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## Cross-references

[Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity](#)  
[Climate Change: Increasing Storm Activity](#)  
[Darwin Point](#)  
[Density and Porosity: Influence on Reef Accretion Rates](#)  
[Midway Atoll \(Hawaiian Archipelago\)](#)  
[Ocean Acidification, Effects on Calcification](#)  
[Oceanic Hotspots](#)  
[Pacific Coral Reefs: An Introduction](#)  
[Submerged Reefs](#)

## HEAVY METAL ACCUMULATION IN SCLERACTINIAN CORALS

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## Synonyms

Heavy metals are also referred to as trace metals or trace elements

## Definition

Heavy metals are metals and metalloids, which have atomic weights between 63.5 and 200.6 g/mol and density  $> 4.5 \text{ g/cm}^3$  (Shah, 2008). Heavy metals are conservative in nature as they persist in the environment for longer periods. Heavy metals are both naturally occurring and anthropogenically introduced in the marine environment and are toxic to both aquatic biota and humans at low concentrations.

## Heavy metals in the marine environment

Elevated concentrations of the heavy metals are the consequence of effluent discharge, urban stormwater, sewage pollution, harbor dredging, sedimentation, and agricultural and industrial runoff. According to Al-Rousan et al. (2007), these heavy metals occur in the coral skeletons as a result of structural incorporation of metals into the aragonite (Goreau, 1977), inclusion of particulate materials in skeletal cavities (reviewed by Howard and Brown, 1984), surface adsorption onto exposed skeleton (St. John, 1974; Brown et al., 1991), and chelation with the organic matrix of the skeleton (Mitterer, 1978). Once incorporated into the coral skeleton, the metals will remain embedded forever since the new growth covers the old carbonate surface (St. John, 1974).

## This study

The metals of interest in this study were copper (Cu), zinc (Zn), lead (Pb), cadmium (Cd), and iron (Fe). Cu, Zn, and

Fe were of particular interest as they are the essential elements required for growth of organisms as well as humans. On the other hand, Cd and Pb, being the non-essential elements, are harmful to the marine organisms due to their polluting effects and toxicity. The concentrations of these metals together with the partitioning of these metals in the skeleton, tissue, and zooxanthellae of three different coral families were looked into. Heavy metal accumulation rates were also studied in the three different families for a 5-day period. Coral samples were taken from three different sites, namely reefs encountering significant terrigenous inputs from rivers, fringing reefs (with a chain of hotels), and a pristine reef.

## Scleractinian corals

*Scleractinian* corals are the architects of coral reefs and hence good indicators of environmental changes due to the fact that their skeletons assimilate records of the presence and concentrations of certain metals over centuries (Esslemont, 1999). Scleractinian corals incorporate the trace elements (or heavy metals) in their living parts and skeletons. *Acropora formosa*, *Pocillopora damicornis*, and *Porites spp.* were studied for heavy metal concentrations.

## Outcomes

High metal concentrations were determined for the zooxanthellae, than the tissue and the skeleton, suggesting that the zooxanthellae are responsible for the metal uptake in corals. Reichelt-Brushett and McOrist (2003) suggest that symbiotic zooxanthellae play an important role in the accumulation and regulation of trace metals. The variation among the three different families of corals suggests that *Porites spp.* tend to accumulate lower concentrations of heavy metals than the other two species studied. Scleractinian corals in pristine environments recorded a lower metal concentration than those obtained from fringing reefs and reefs closer to significant terrigenous inputs.

Fe and Pd were found to be in higher concentrations than Cu, Zn, and Cd at all the study sites. The most probable reason that Fe reaches the marine environment is through suspended sediments and aeolian dust. Fringing reefs and reefs near terrigenous inputs have constant influences of suspended sediments and hence it is most likely that Fe enters the marine environment through this means. High concentrations of lead in the samples were mostly from sewer outfall, industrial discharge, and agricultural/storm water runoff and wastes discharged from hotels and piggery farms.

Dose-response curves from the bioassays showed that as the nominal concentrations increase, the heavy metal uptake in corals also increases. Zooxanthellae were lost to the aquaria water as a result of stress on the corals. High concentrations of Pb and Fe were accumulated in the corals for each dosage period.



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## HISTORICAL ECOLOGY OF CORAL REEFS

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### Definition

Historical ecology: Using time-series data collected over single or multiple temporal scales to lend insight into the history of modern communities and ecosystems.

### Introduction

The diversity, frequency, and scale of human impacts on coral reefs are increasing to the extent that reefs are threatened globally (Wilkinson, 2008). The direct and indirect effects of overfishing and pollution from agriculture and land development have been the major drivers of massive and accelerating decreases in abundance of coral reef species (Moberg and Folke, 1999; Abram et al., 2001; Jackson et al., 2001; Gardner et al., 2003; Hughes et al., 2003; Pandolfi et al., 2003). These human impacts and the increased fragmentation of coral reef habitat are unprecedented and have the possibility to undermine reef resilience (Bellwood et al., 2004), raising the likelihood that modern coral reefs might be much more susceptible to current and future climate-change than is suggested by

their geologic history (Hughes et al., 2003; Bellwood et al., 2004).

One of the most urgent questions in conservation science is: What was natural in the world before humans impacted it? Study of past ecosystem condition and the relationship between ecosystem health and human–ecological interactions provides a way to gain insight into what was natural in the sea. Historical ecology is the name generally given over to such study. It provides a basis for avoiding the “shifting baseline syndrome” (Pauly, 1995) which undermines current perspectives on what constitutes a pristine ecosystem.

The conceptual framework surrounding historical ecology finds its roots in Aldo Leopold who in 1941 called for study of wilderness areas, for “. . . a science of land health needs, first of all, a base-datum of normality, a picture of how healthy land maintains itself. . .” (p. 3). Several papers on terrestrial ecosystems in the early 1990s have set the tone of historical ecology (Morgan et al., 1994; Swetnam et al., 1999). In general, historical ecology links past ecosystem condition with the present state using time series data over a number of temporal scales, from decades to millennia, though shorter term studies conducted over discrete time intervals can also be used. Insights generally sought over the long temporal frames of historical ecology include changes in states of populations, species, and ecosystems (e.g., abundance, biomass, geographic ranges), changes in environmental parameters (e.g., sea surface temperature fluctuations), and changes in magnitudes and rates of both biological (e.g., mortality rates, trophic flows, disturbance regimes) and physical (e.g., El Niño–Southern Oscillation, climate change) processes.

### The tools of marine historical ecology

Practitioners of marine historical ecology on coral reefs use a number of different kinds of data from multiple time periods to examine the recent past history and present condition of reef ecosystems to provide a natural baseline for community ecology and coral growth rates. Archaeological sites provide insight into the relationship between the development of civilization and its evolving impact on coastal marine resources. Historical records such as those found in ships logs, and publications of early naturalists and European colonialists provide a moving window of the natural history and inferred ecology of many coral reef inhabitants. Fisheries records and modern ecological surveys can be used in association with remote sensing data (going back the last 20 or 30 years) to provide a detailed picture of changing environments and biodiversity as human population and consumption, as well as economic globalization, have accelerated during the past several decades. Taken together, these databases provide a holistic view of changing environments and ecology on coral reefs that includes the onset of human disturbances and against which the acquisition of present day data can be evaluated.

Paleontological (Aronson and Precht, 1997; Wapnick et al., 2004; Pandolfi and Jackson, 2006), archaeological (Erlandson and Rick, 2008), historical (Starkey et al., 2000; Bolster, 2006; Lajus, 2008), ecological (Greenstein et al., 1998; McClenachan et al., 2006), genetic (Roman and Palumbi, 2003; Alter et al., 2007), and modeling studies are all contributing to a new awareness of the past bounty and diversity in the sea (Jackson, 2008; Pinnegar and Engelhard, 2008). Historical data sources include oral histories (Dulvy and Polunin, 2004), photographs (McClenachan, 2009), museum records (Robinson and Frid, 2008), early scientific studies (Lajus et al., 2007), fisheries information including logbook data (Klaer and Polacheck, 1997), landings, effort, and gear (Bager et al., 2007; Lotze, 2007; MacKenzie et al., 2007), and fishing charts (Claesson, 2008). Historical studies are limited to the periods of time and geographic areas for which data are available (MacKenzie et al., 2007). Some studies are limited to more recent history (McClenachan, 2009), while others date back to the sixteenth century (MacKenzie et al., 2007). Many fisheries records are only available for disjointed time periods (Gaumiga et al., 2007; MacKenzie et al., 2007), while others provide continuous time series lasting over a hundred years (Holm and Bager, 2001; Lajus et al., 2007). Some data sources provide only a snapshot of past conditions such as journal entries and photographs; however, when viewed together over a period of time such information can reveal substantial changes in marine environments (Jackson, 1997).

### Historical ecology of coastal ecosystems

Recent papers on the historical ecology of coastal ecosystems have demonstrated the importance of time-series data to understanding the ecology and degradation over long temporal scales. For example, by employing a multi-disciplinary approach involving ecologists, oceanographers, archaeologists, and social scientists, Jeremy Jackson and his colleagues (Jackson et al., 2001) investigated the ecological history of coastal ecosystems worldwide. The work documents in broad terms the history of human alterations in the sea, identifying overfishing as the first and farthest reaching cause of decline in coastal marine ecosystems. Historical marine ecology has since investigated a broad range of ecosystems and problems in the sea (for recent review see Lotze and Worm, 2009).

### Key findings on coral reefs

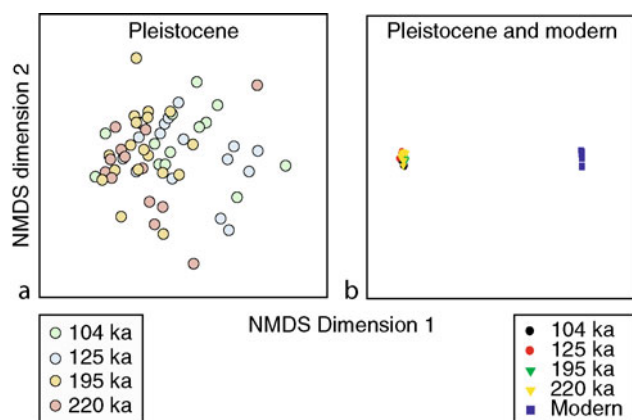
Study of coral reef ecosystems has also been subject to the “shifting baseline syndrome” – coral reef systems have undergone systematic degradation prior to recent ecological studies in the last three or four decades. This strongly implies that no reef can be considered “pristine”, and that no standard exists by which to compare the magnitude of these changes (Jackson et al., 2001). Through paleoecological reconstruction of coral reefs from the Caribbean region, recent studies have highlighted the collapse of coral communities at a regional level, which is unprecedented

within the Holocene (12,000 years ago – present), (Greenstein et al., 1998; Aronson et al., 2002) and Pleistocene (1.8 million – 12,000 years ago), (Jackson, 1992; Greenstein et al., 1998; Pandolfi, 2001; Pandolfi and Jackson, 2006).

Very recent work has sought to understand human impacts by developing time-series data archives that can be used to evaluate trends in the global decline of coral reefs since the arrival of humans (Pandolfi et al., 2003; Daley et al., 2008). Study of the historical ecology of coral reefs, relying on the past history of corals and other components of the reef ecosystem showed that the history of ecosystem changes among 14 different tropical reef sites worldwide, with early and effective overfishing as the major culprit in reef decline (Pandolfi et al., 2003; Pandolfi et al., 2005). These findings point to the immense importance of understanding historical events when attempting to tease out factors that have influenced or may influence present coral reef biodiversity (Pandolfi et al., 2003). By considering these global “ecological trajectories” in the light of potential responses to projected global climate change, the history of human exploitation can be linked with global environmental parameters (Hughes et al., 2003). Knowledge of past ecosystem states provides at the minimum, an understanding of what was natural and may even aid in assessing the success of management toward particular conservation goals.

Numerous other smaller scale studies have been undertaken on individual reefs and reef areas around the world, including Hawaii (Herman, 1979), the Great Barrier Reef, (Daley et al., 2008), Florida (McClenachan, 2009), Bahamas (Blick, 2007), Solomon Islands (Aswani and Hamilton, 2004), Indonesia (Palomares et al., 2007) and the Caribbean (Jackson, 1997; McClenachan et al., 2006). The demise of many coral reef fisheries has been traced to their historical beginnings including Florida sponges (McClenachan, 2008), Caribbean turtles (McClenachan et al., 2006) and monk seals (McClenachan and Cooper, 2008), sea turtles in Oceania (Allen, 2007), and Hong Kong fisheries (Cheung and Sadovy, 2004). Through these studies, there is now general recognition throughout the coral reef scientific and management communities of the importance of considering changes in ecosystem state over appropriate time scales (Dulvy and Polunin, 2004; Knowlton and Jackson, 2008; Pinnegar and Engelhard, 2008). Importantly, there is far greater appreciation of the historical development, timing, and ecosystem responses to the ultimate drivers of coral reef ecosystem decline, namely overfishing (Roberts, 2007), climate change (Hughes et al., 2003), and coastal development and pollution (Ramade and Roche, 2006).

An understanding of the history of reef coral communities can aid conservation initiatives by supplying information on natural baselines in the sea that are immune to the “shifting baseline syndrome”. For example, in Barbados coral community composition was very similar during four separate reef-building episodes between 220 ka and



**Historical Ecology of Coral Reefs, Figure 1** Non-metric multi-dimensional scaling (NMDS) ordination of the relative abundance of the common coral taxa in Pleistocene and modern assemblages from Barbados, West Indies. (a) Coral assemblages aged 104, 125, 195, and 220 ka from the Pleistocene leeward reef crest of Barbados. (b) Combined analysis of Pleistocene and modern coral assemblages surveyed in the 1980s by Tomascik and Sander (1987) (from Pandolfi and Jackson, 2006).

104 ka (thousand years ago) (Pandolfi and Jackson, 2006), and community structure is now very different in modern degraded habitats (Lewis, 1960, 1984; Tomascik and Sander, 1987) (Figure 1). The same six most common coral species comprise >97% of the total coral density in the fossil assemblages: *Acropora palmata*, *A. cervicornis*, organ-pipe *Montastraea*, *M. annularis* s.s., *Diploria strigosa*, and *M. faveolata*. *Acropora palmata* was overwhelmingly the most abundant species at all four time periods. In marked contrast to the Pleistocene coral assemblages, those from the living reef on Barbados are dominated by species that were rare in the Pleistocene communities. The most abundant coral is *Porites astreoides*, followed by *P. porites*, *Siderastrea radians*, and *Agaricia agaricites*. Living communities contained very little *A. palmata* and no *A. cervicornis*. Similar contrasts between ancient and modern assemblages have also been derived from reef framework cores taken from the nearshore Great Barrier Reef (Perry et al., 2008; Pandolfi et al., 2009).

### Management implications

The descriptive side of marine historical ecology has been vigorously pursued, especially after the publication of Jackson et al. (2001). This has been confined mainly to admonitions about how resources “then” were unimaginably greater than they are “now” (summarized in Lotze and Worm, 2009). But marine historical ecology has lagged behind its terrestrial counterpart (Swetnam et al., 1999; Froyd and Willis, 2008) in harnessing the enormous scope and information potential of direct import to the understanding and management of marine environments. This has resulted in several disadvantages to coral

reefs and our understanding of them: (1) management without a temporal context; (2) a diminished ability to differentiate between chronic and cumulative impacts; (3) uncertainty in attributing ecological changes to human or natural agency; (4) encouraged equilibrium views of ecosystem dynamics; and (5) difficulty in setting management goals and assessing the effectiveness of management actions.

The challenge for natural resource managers is in understanding where the ecosystem they are managing stands in relation to its natural state. Historical knowledge of ecosystems is critical for understanding natural variability and temporal dynamics and provides an essential bridge between science and management goals and outcomes. More positive outcomes are possible when managers possess clear goals for ecosystem restoration derived from knowing how different today’s oceans are from their pristine condition.

### Summary

Seascapes, nearly anywhere you care to investigate, have undergone undeniable transitions from “nature-dominated” to “human-dominated” regimes (Figure 1). Knowing the nature and timing of these transitions cannot be attempted outside of a historical context. How do humans interact with seascapes? How long ago was this interaction first detectable? Lengthening the temporal scale of ecological studies affords the opportunity to debate the characteristics of the transition from nature to human-dominated seascapes along slowly changing gradients. It is also of critical importance to reef management for (1) identifying drivers of ecosystem change, (2) providing meaningful goals for successful management and a means for measuring success of management actions, and (3) adopting a dynamic view of ecosystems.

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## Cross-references

[Conservation and Marine Protection Areas](#)  
[Heavy Metal Accumulation in Scleractinian Corals](#)  
[Paleoclimate from Corals](#)  
[Reef Restoration](#)  
[Sediment Durability](#)

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## HOLOCENE HIGH ENERGY WINDOW

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## Definition

*Holocene high energy window*: A period of higher wave energy conditions across submerged reef or continental

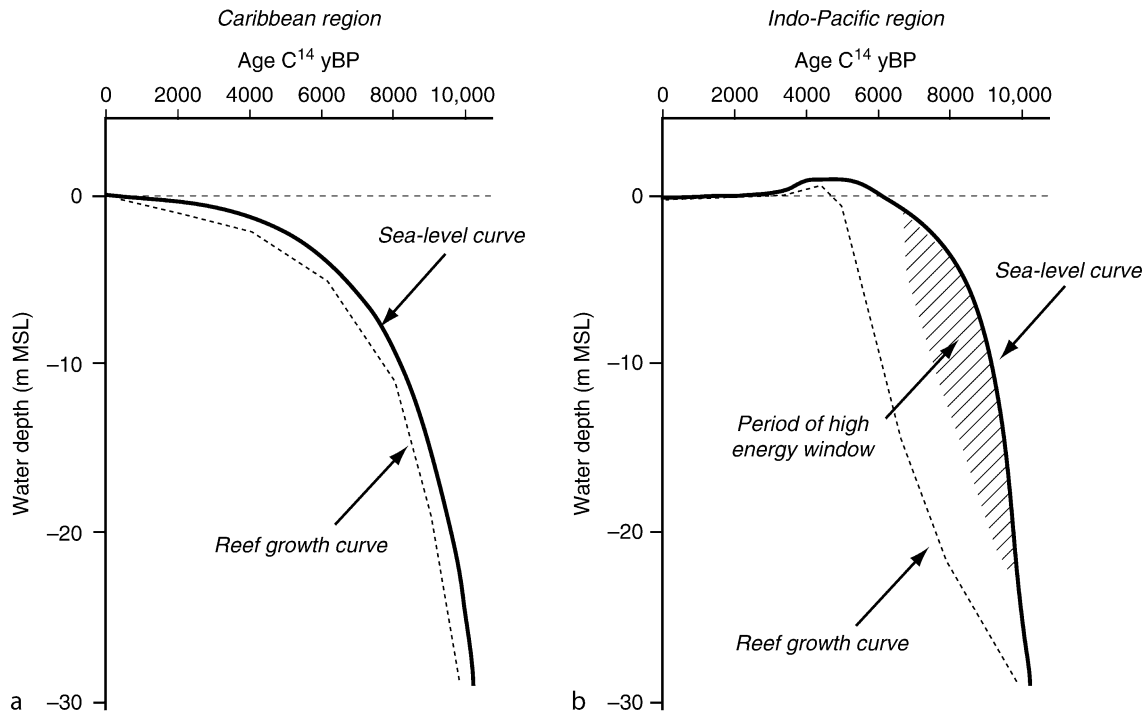
shelf environments that was caused by reef growth lagging behind rising sea levels during the Holocene transgression.

## Introduction

The concept of a Holocene “high energy interval” or “window” was first introduced by Neumann (1972) as a mechanism to explain the emplacement of relict sedimentary deposits that appeared to have formed under higher energy conditions than those prevalent in the present. Specifically, it was suggested that these deposits might have formed during periods when coastlines were less protected than at present. This concept was subsequently developed by Hopley (1984) as a potential control on the nature and character of shelf sedimentary environments, using Australia’s Great Barrier Reef (GBR) shelf as an example. Such temporal changes in energy conditions are believed to have occurred in settings where the outer shelf or barrier reefs failed to keep pace with rising sea levels during the Holocene transgression. Rather they adopted “catch-up” (*sensu* Neumann and Macintyre, 1985) growth trajectories, with the lag interval providing a depth window through which waves could propagate across both developing reef surfaces and wider shelf sedimentary systems. The legacy of this is seen today as the occurrence of high energy sedimentary deposits that could not have formed under present energy regimes. As reef growth reached present sea-levels the “window” was progressively shut resulting in reduced wave energy conditions to leeward of reef crests or across open shelf environments and a consequent transition in styles of reef growth and sediment accumulation.

## Global and regional scale perspectives

The potential for the occurrence of a high energy window during the Holocene transgression was entirely controlled by the interactions that occurred between the rate of coral reef growth and the rate of sea-level rise. These interactions must, inevitably, have differed between reef sites and on a regional basis, and thus the potential for the occurrence, and longevity of any higher energy periods must have been spatially very variable. For example, in the Caribbean region, reconstructed Holocene sea-level curves show that rates of sea-level rise have steadily fallen since ~10,000 years BP (when sea level was at ~–24 m below present) through to the present day. Rates of rise averaged ~5.2 mm year<sup>–1</sup> up until ~8,000 years BP, ~1.5 mm year<sup>–1</sup> from about 8,000 to 4,000 years BP, and 0.93 mm year<sup>–1</sup> from 4,000 years BP to present (Toscano and Macintyre, 2003). Taking a modal long-term rate of reef accretion of ~6–7 mm year<sup>–1</sup> (e.g., Montaggioni, 2005) most reefs would have had the potential to track rising sea-levels (“keep-up” growth mode: *sensu* Neumann and Macintyre, 1985), thus minimizing the potential for the development of a high energy window (Figure 1a). In contrast, rates of sea-level rise during the early phases of the Holocene transgression were much faster in much of the Indo-Pacific basin (Camoin et al., 2004).



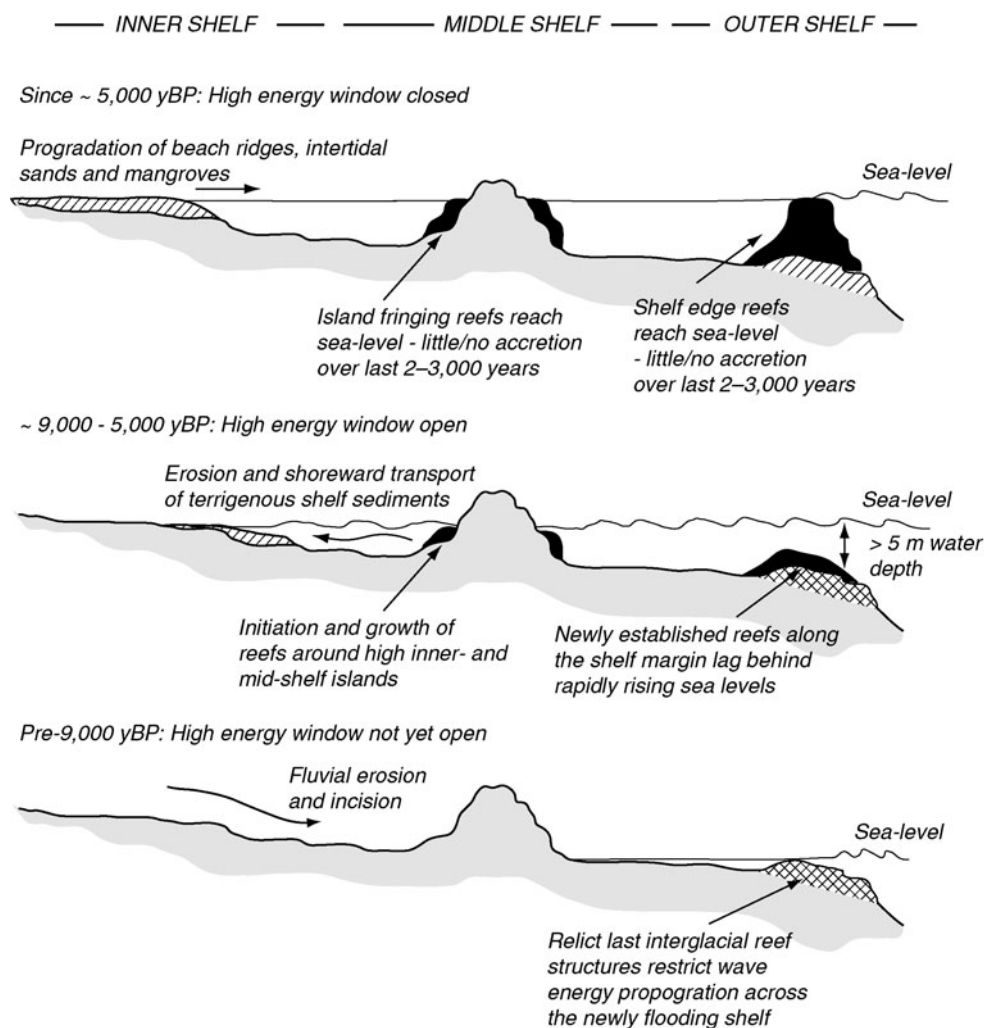
**Holocene High Energy Window, Figure 1** Regional variations in the potential for the existence of a Holocene high energy window for (a) the Caribbean, and (b) the Indo-Pacific regions (based on sea-level curves from the central Great Barrier Reef Shelf, Australia). Note that under scenario (b) reef growth lags a rapidly rising sea level, providing a window for high wave energy propagation across the shelf.

In eastern Australia, for example, where Hopley (1984) discussed the potential for the development of periods of high energy conditions during shelf flooding, sea-levels during the early-mid Holocene are estimated to have been rising at  $\sim 10 \text{ mm year}^{-1}$  from about 9,000 to 7,500 years BP, and then at  $\sim 2\text{--}2.5 \text{ mm year}^{-1}$  through to  $\sim 6,000$  years BP when sea levels slightly exceeded their present day position. Since this, highstand sea-level has fallen to its present level. This faster rate of sea-level rise during the early-mid-Holocene period is believed to have resulted in reef growth lagging behind sea-level, thus temporarily allowing higher wave energy regimes to propagate across reefs and the inundating shelf environments (Figure 1b). However, as plots of sea-level position against reconstructed reef growth trajectory plots demonstrate, the potential for the development of a high energy window appears very variable even at an intra-regional scale (Camoin et al., 2004).

The existence of such a high energy window has been most widely discussed in relation to the GBR shelf of Australia (Hopley, 1984; Hopley et al., 2007), although the timing and existence of such a window probably varied at different points along the shelf. This has been viewed, in large part, as a function of variations in the depth from which Holocene reef growth was re-establishing - those areas with deeper Pleistocene foundations having greater potential to adopt catch-up growth modes as they lagged behind sea-level (Hopley et al., 2007). For example, along

the northern and southern sections of the GBR reef establishment occurred above foundations at depths of  $\sim 15\text{--}20 \text{ m}$  and the high energy window is inferred to have been open only for a relatively short period of time between  $\sim 8.0$  and  $6.0 \text{ ka}$ . In contrast, the greater depth ( $\sim 20\text{--}25 \text{ m}$ ) of the Pleistocene foundations in central areas of the GBR means that the window may have been open for longer. In this area of the shelf, the occurrence of relict Pleistocene reefal substrates along the shelf margins is believed to have protected the newly submerging shelf from high wave energy conditions prior to  $\sim 9,000$  years BP (Figure 2). However, from about 8,500 years BP these relict reef structures were progressively over-topped as newly established outer-shelf reef growth lagged behind rapidly rising sea levels. The result was a marked increase in energy levels across the newly submerged shelf, with important impacts on mainland coast and shelf sediment dynamics. Significant onshore transport of coarser-grained sediments is believed to have occurred during this period, and has been cited as a causal factor in the deposition of high energy features such as boulder beaches and spits around some of the inner-shelf high islands (illustrated in Hopley et al., 2007, fig 7.4). Also during this time significant onshore migration of reworked terrigenous shelf sediments is believed to have occurred, producing the presently well-defined inshore terrigenous sediment prism (Larcombe and Woolfe,





**Holocene High Energy Window, Figure 2** Schematic diagram showing the influence of a Holocene high energy window on the development of shelf environments based on the central Great Barrier Reef region of Australia (stage concepts developed from Hopley, 1984; Hopley et al., 2007).

1999). During the final stages of the transgression, when present sea-levels were reached (or exceeded), reefs along the outer-shelf margin caught up with sea-level, leading to closure of the high energy window. Numerous headlands were incorporated into the coast during the final stage of the transgression resulting in the development of a much more indented coastline. This facilitated the trapping of longshore-driven sediments and the development and progradation of extensive coastal beach ridge sequences.

### Impacts of a high energy “window” at the reef and reef island scale

Whilst the concept of a Holocene high energy window is perhaps best known from discussions regarding its influence on the GBR shelf, the concept has also been considered in relation to different phases of reef and reef island development. This is evident, for example, along

reef-fronted coastlines and narrow shelves where reef growth appears to have lagged behind sea-level. Subsequent accumulation of barrier-type reefs up to sea-level resulted in a closure of these more localized high energy windows, leading to a transition in the nature and character of reef-building to leeward of the main reef structures. Examples include those reefs described from the Ryukyu Islands (Kan et al., 1997), Palau (Kayanne et al., 2002), and Madagascar (Camoin et al., 2004). The concept of high energy phases has also been discussed as an important potential control on reef island building. Kench et al. (2005), for example, have invoked periods of higher wave energy and associated sediment transport to nodal sites of accumulation, as an important control on the development of reef islands in the Maldives. Similar views have also been discussed in relation to a range of reef islands in the Pacific (Nunn, 1997) and on the GBR (Hopley, 1984).

## Summary

The concept of a Holocene high energy window has been evoked to explain the presence of sedimentary deposits that appear to have formed under higher wave energy conditions to those operating in the present. Such periods of higher energy can occur where vertically accreting reefs lag behind rapidly rising sea levels – thus opening up the potential for wave energy to propagate across both reef structures and adjacent shelf environments. Such periods of higher wave energy have been invoked in a number of areas where rapid rates of sea-level rise occurred in the early-mid Holocene, and discussed in relation both to large shelf systems, and the development of reefs and reef islands. However, spatial variations in the rate and timing of the post-glacial marine transgression, and variations in the depth of the substrates over which flooding occurred, means that the extent and longevity of any such window was probably highly variable between regions. Of interest in the context of near-future environmental change is the idea that such high energy windows may once again open up across reefs where the combined effects of environmental and anthropogenic disturbance interact to suppress reef growth potential (or even to drive reef erosion). Under such scenarios reefs may not be able to respond to even modest rises in sea level, thus allowing greater wave energy transfer across reef flats (see Sheppard et al., 2005). Where this occurs there will be obvious implications for lagoon and island sediment dynamics and shoreline stability.

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## Cross-references

[Accommodation Space](#)  
[Antecedent Platforms](#)  
[Boulder Beaches](#)  
[Boulder Zone/Ramparts](#)  
[Climate Change: Increasing Storm Activity](#)  
[Postglacial Transgression](#)  
[Sea Level Change and Its Effect on Reef Growth](#)

## HOLOCENE REEFS: THICKNESS AND CHARACTERISTICS

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Continuous coral reef growth since the last glacial lowstand of sea level some 18 kyrs BP has been documented by drilling around the islands of Barbados (Fairbanks, 1989) and Tahiti (Bard et al., 1990). In the majority of cases investigated though, shelf reefs started to accrete not earlier than the Holocene (< 10 kyrs BP). Holocene reef thickness and accretion-rates exhibit large variation and can be as high as > 40 m and > 20 m/kyr, respectively (Dullo, 2005; Montaggioni, 2005). Scoffin (1992) has summarized how the synchronously operating processes of framework growth, bioerosion and breakage (reef destruction), encrustation, loose sediment accumulation, and cementation have resulted in late Quaternary reef accretion. A number of external factors such as antecedent topography, water temperature, nutrient concentrations, and exposure to waves and currents influence Holocene reef growth; however, sea level appears to exert major control. Neumann and Macintyre (1985) have elegantly categorized reef response to postglacial sea-level rise into keep-up, catch-up, and give-up reef anatomies. The keep-up type is characterized by branched acroporids and the catch-up type by branched and/or massive corals and shallowing upward facies. The give-up type shows

a deepening upward facies and the reef top is located in deeper water, in contrast to the keep-up and catch-up types where the reef top is more or less at sea level. Recently, Gischler (2008) and Hubbard (2009) have shown for the western Atlantic that Holocene reefs dominated by acroporids do not accrete faster as compared to massive coral reefs, even though acroporid corals exhibit growth-rates one magnitude higher as compared to massive corals. Also, reef accretion-rates did not correlate negatively with increase in paleo-water depth over an investigated range of 25 m. An explanation for these unexpected results might be that the effects of destructive processes in reefs decrease with depth. First, massive corals are more resistant and accrete with little disturbance in deeper water whereas shallow water acroporids are repeatedly leveled by cyclones. Second, current knowledge indicates that rates of bioerosion apparently decrease with increasing water depths. These findings also contribute to the question as to how much of a reef is represented by *in situ* framework and what percentage comprises transported detritus, a question that has been discussed for over a century by reef workers (e.g., Hubbard, 2009). It seems that in Holocene reefs – and possibly the same holds true for their fossil counterparts – detritus clearly exceeds autochthonous framework, and destructive processes are an integral component of reef accretion.

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## Cross-references

Barbados  
 Bioerosion  
 Eastern Caribbean Coral Reefs; Eastern Tropical Pacific Coral Reefs  
 Indian Ocean Reefs  
 Pacific Coral Reefs: An Introduction

## Reef Structure

Sea Level Change and Its Effect on Reef Growth

Sediments, Properties

Submarine Lithification

Tahiti/Society Islands

Taphonomy

Western Atlantic/Caribbean, Coral Reefs; Eastern Caribbean Coral Reefs

## HUON PENINSULA, P.N.G.

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Huon Peninsula on the northeastern coast of Papua New Guinea is located at the overriding South Bismarck plate on the Australian plate and at 6°S. This tectonic and latitudinal setting allows the formation of spectacular uplifted coral terraces, which are regarded as one of the standards for eustatic sea level changes superposed on tectonic uplift (Chappell, 1974; Chappell and Shackleton, 1986). Terraced area ranges from ca. 2 to 15 km in width, separated by NW–SE trending Kalasa Fault from the Cromwell Range. However, Kalasa Fault partly truncates older terrace (Terrace XIV or XV), and branches into two on the southeastern end, cutting younger terraces.

The major coral terraces, I–XV in ascending order, record the high sea level of interglacial period and are constructional terraces underlain by coral limestone with transgressive facies, correlated with MIS 1 to 14 (Figure 1). Correlation of each transgressive terrace with MIS is supported by many U-series dates for Terrace VII and younger terraces (Chappell et al., 1996; Yokoyama et al., 2001; Cutler et al., 2003); however, older terraces are not well dated. Terrace VII (MIS 5e, ca. 124 ka) is especially continuous, and its height shows northward down tilting from ca. 400 to 50 m over ca. 70 km long coastline with the maximum uplift rate of 3.3 m/1,000 years. Preservation of original terrace surfaces is closely related to the amount of uplift and age of terraces. Holocene terrace of MIS 1, dated by radiocarbon method at many sites, also tilts from 25 to 5 m. Maximum height of preserved terrace XV is ca. 1,500 m. Formation of multiple terraces, including those for the relatively low sea level (MIS 5c, 5a, and 3), is resulted from such a high uplift, which has continued throughout the middle Quaternary.

The rapid uplift of the peninsula is associated with the repeated coseismic uplift, which is expressed by a series of small terraces cutting into the major terraces (Ota et al., 1993). Coseismic uplift has an order of 2–5 m in magnitude and ka order of repeat time, judging from the terrace height and ages. Coseismic uplift is recorded not only in the Holocene terrace but also in late Quaternary terraces (Ota and Chappell, 1996). This is very unique phenomenon caused by the good preservation of coral limestone resistant to physical weathering.





**Huon Peninsula, P.N.G., Figure 1** View of coral terraces at the Huon Peninsula. (Photo by Ota.)

Morphology of major terraces is characterized by the prominent barrier, lagoon, and barrier following streams. Presence of dense short gullies also characterizes the morphology of terrace risers. Doline is often seen on very extensive Terrace X and XI. Landslides and related debris flows, destructing or overlying the coral terraces, also provide characteristics features, many of which can be regarded by paleoearthquake (Ota et al., 1997).

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### Cross-references

[Emerged Reefs](#)  
[Pacific Coral Reefs: An Introduction](#)  
[Uranium Series Dating](#)

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## HYDRODYNAMICS OF CORAL REEF SYSTEMS

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### Synonyms

Coral reef hydrodynamics; Currents on reefs; Water flow over coral reefs

### Definition

Hydrodynamics. The science of water flow and the forces that cause that flow.

### Hydrodynamics of coral reef systems

#### Water flow in coral reef systems

Coral reef systems are spatially inhomogeneous and consist of an amalgam of sub-systems, which have different benthos and widely varying geomorphology. These include the reef, or reefs, one or more lagoons, and regions of the neighboring ocean that are affected by the reefs. All

of these sub-systems are connected hydrodynamically by processes on the reef and these processes are the focus of the present article. Much of what happens on the reef, in terms of hydrodynamics, is controlled by the topographic complexity of the reef and is also affected by the surrounding environment of the reef system. Our attention is primarily directed towards shallow reefs and these may be either sub-tidal, or inter-tidal. Reefs may have varying types of benthos (coral, algae and sand) and are zoned in a way that affects bottom friction and many other aspects of their hydrodynamics. A recent survey of coral reef hydrodynamics is given by Monismith (2007).

Coral reef hydrodynamics differs in many important respects from the hydrodynamics of other coastal systems and these differences will be discussed here. The science of water flow over reefs is the cornerstone of much of our understanding of the ecology and biogeochemical dynamics of reefs. Its effects are multifarious and occur at many space and time scales. Coral reefs efficiently dissipate wave energy and constitute some of the best submerged breakwaters in the natural world (von Arx, 1948). This creates low-energy lagoons, which are fed with water from the reef (Hench et al., 2008) and also have their own patterns of water circulation (“entry lagoons”; “entry lagoon circulation”). Reef hydrodynamics can be greatly affected by conditions in the lagoons, and the outside ocean, and there are processes of continual recirculation of water that are augmented by astronomical tides.

Coral reefs have high biological productivity that is the marine equivalent of tropical rain forests (Hatcher, 1998). There are many similarities between the two systems: the structural complexity of reefs seems to have an important analog in tropical rain forests with the same degree of ecological complexity and biodiversity (Brown et al., 2002). At the heart of the processes which control such productivity are the dynamics, transport and recycling of nutrients and their dependence on the hydrodynamic processes at a variety of space and time scales (Hatcher, 1997). This includes all of the complex small scale vortices, and wave motions found on reefs, which are part of the turbulence field. Unlike most coastal systems, the spectrum of significant topographic complexity in reefs appears almost continuous from scales of hundreds of meters down to millimeters. There is a possible distinct change in the nature of this complexity at the scale of individual coral colonies and this is a physical scale that can be utilized in conceptual (and numerical) models of reef hydrodynamics.

Reef currents are produced by many types of environmental forcing of which the most important are breaking surface waves (“entry Waves and wave driven currents”), astronomical tides, and wind stress (Munk and Sargent, 1954; Kench, 1998). Other influences may also be present on some reefs such as the thermohaline processes (Monismith et al., 2006) and long period ocean oscillations; for the Great Barrier Reef see the excellent volume by Hopley et al. (2007). Of all these forcing processes, the most important is wave breaking and the

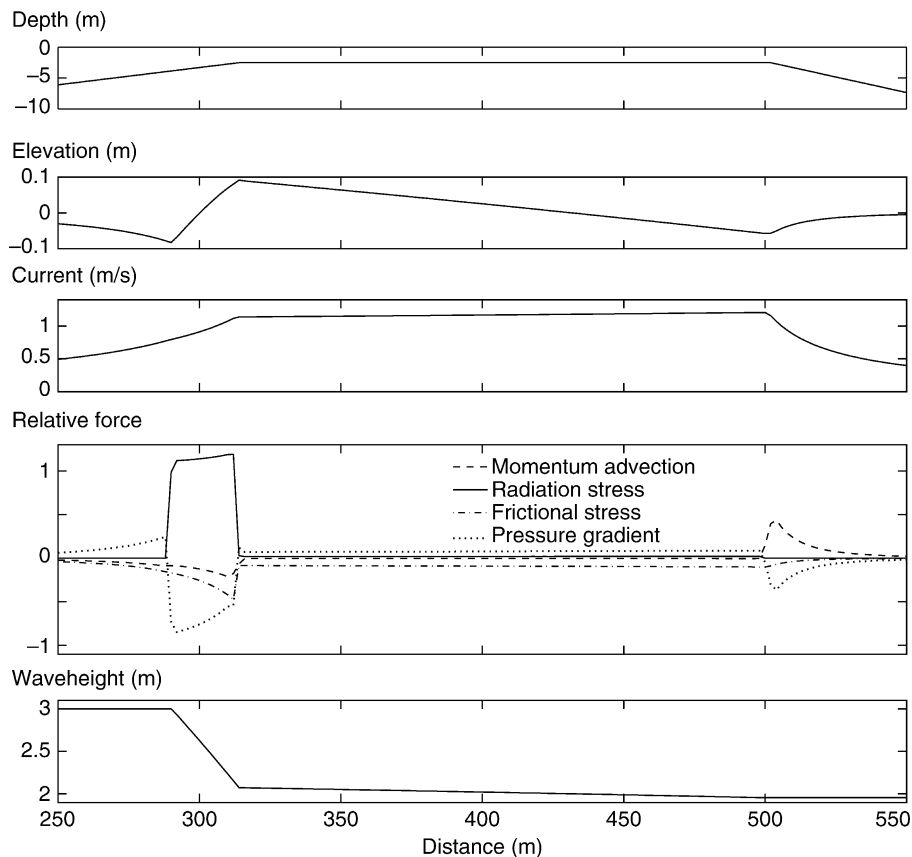
quintessential, and fundamental, problem of water flow in coral reefs involves waves breaking on a well-defined fore-reef (“entry Fore reef/reef front”) and flowing across the adjoining reef flat into a lagoon. The waves are usually ocean swell but can be wind waves (Kraines et al., 1998). This topography fits many reef systems and has been studied through conceptual and numerical models by Tait (1972); Symonds et al. (1995); and Hearn (1999) and recently reviewed by Monismith (2007). This “classical reef flow” problem is illustrated in Figure 1 and we shall discuss this prototype of all reef models in some detail.

There are two basic conceptual models of the physical structure of a coral reef. The first is the “solid reef model,” in which the reef is represented as a solid body (without reentrant surfaces in the vertical plane) to which are added “roughness elements.” This can alternatively be described as a “bathymetry model” since it can be totally described by a conventional bathymetry dataset with depth as a function of horizontal position. It is discussed in the following sections. The other type of model is the “porous reef model” mentioned later in this article. These conceptual models, which are used for analytical and numerical simulations, have been accompanied by so-called “physical models” built in many laboratories and also, at larger scale, as the coral reef mesocosm at the Biosphere 2 facility in Arizona (Atkinson et al., 2001). Such physical models provide much important hydrodynamic, chemical and biological data although there is limited guidance as to the correct physical, and ecological scaling parameters to be used in this model building.

In the solid reef model, the reef can, in principle, be treated by conventional coastal models (Peterson et al., 2006; Hearn, 2008). However, there are many aspects of flow over a reef that make it distinct from conventional coastal flow and these will be explored in this article.

### Friction on reefs

Part of the hydrodynamic uniqueness of coral reefs is that they are submerged natural structures that have the same efficacy as do solid barriers in dissipating ocean waves and creating calm lagoons. Their dissipation of waves is due to a resistance to water flow that can be treated as friction although it cannot be purely “skin friction” as in most coastal models. Instead, the friction comes primarily from “form drag” created by the irregularity and complexity of the structure. In solid reef models, the friction offered by reefs is created by the “roughness elements.” The simplest representation of such friction is a frictional drag coefficient. Approximate coefficients for bottom friction on reef flats were originally derived from field data relating incoming wave height and reef current (Hearn, 2008). A coefficient of friction for coral can also be obtained by measuring the current produced by a known head of water in a flume filled with living coral cut from a reef (Atkinson and Bilger, 1992). It is also possible to estimate friction coefficients from acoustic measurements of current either using profiles of current against height or by determining



**Hydrodynamics of Coral Reef Systems, Figure 1** The classical reef problem showing a typical reef with water elevation, current, relative dynamical forces and wave height.

the Reynolds stress. A review of some of this work, is given by Monismith (2007). These methods give values of quadratic friction coefficient of the order 0.01–0.1 compared with a typical value of 0.0025 for the skin friction from sand particles in coastal waters.

The use of a drag coefficient is rather limited for several reasons. Firstly, it follows from the theory of the logarithmic layer, that the coefficient will always increase as water depth decreases and so a comparison between values in the scientific literature necessarily requires a knowledge of that depth. Secondly, as discussed later in this article, the presence of waves causes the quadratic dependence of frictional stress to fail at low currents. Finally, the height of the “roughness elements” on reefs is necessarily an appreciable fraction of the height of the water column so that the simple models that lead to quadratic friction in coastal models are not completely applicable.

The part of the bottom of the water column around the roughness elements is called the “roughness layer” and fluid flow in this region is complex and dominated by inertia forces. We are only now starting to understand how to model water flow within the roughness layer and there are some similarities here with flow through canopies formed by submerged aquatic vegetation (Cornelisen and

Thomas, 2009). Experiments have been performed within flumes although the experimental reef structures built in the laboratory can lack important aspects of the real structural complexity found in nature.

Solid reef models, can accommodate some part of the processes within the roughness layer by a phenomenological modification of the Prandtl formulation of a vertical “mixing length.” For a roughness layer that is thin (compared to water depth), this mixing length method reproduces the familiar logarithmic layer profile of current against height within the water column. In such cases, measurement of this profile is a valuable method of finding the roughness lengths (Lacy et al., 2005). The value of the mixing length concept is that for a thick roughness layer, it can be modified so that, within the roughness layer, it has a polynomial dependence on height (Hearn, 2008).

### Spatial variability of roughness

#### Rough reef flat

The original solutions of the classic reef problem, illustrated in Figure 1, simply assumed that the drag coefficient, or roughness length, for the reef flat was the same as that on the fore-reef. This creates a balance of forces



on the fore-reef which is mainly between radiation stress and pressure gradient. The radiation stress is a representation of the force from breaking waves and the pressure gradient is due to a build up of water in the direction of those breaking waves called the “wave set up” (“entry Wave set up”). This results in the water level at the reef crest being higher than the outside ocean by as much as tens of centimeters. A similar effect can be seen on a seawall as waves break against it. This wave set up then causes water to flow across the reef flat, i.e., there is a pressure gradient across the reef flat which is balanced by the friction created by the current. Although smaller waves propagate across the reef flat, wave breaking there is very limited.

The zone of breaking waves is called the “surf zone” and is the most easily recognized region of a coral reef with its line of white breakers. The width of the surf zone is controlled by the height of incoming waves (usually swell) and the slope of the fore reef. The width varies greatly amongst the coral reefs of the world. Fore reefs with steep slope have narrow surf zones while gently sloping fore reefs have much wider surf zones. The current that is forced across the reef flat by the breaking waves originates in the region beyond the surf zone. It must then pass through the surf zone, onto the reef flat, and out to the lagoon where it returns back to the surrounding ocean. This essentially creates a large circulation cell, or a series of cells, the sizes of which are mainly controlled by the morphology of the lagoon. Circulation in the cells becomes very dispersive in the deeper ocean outside of the reef system. Water may also form closed gyres, or eddies, on the reef itself because the wave set up can vary laterally along the line of the reef crest. Water also flows laterally along the fore reef. The extent of this lateral flow is controlled by the lateral bathymetry and friction (which may be highly anisotropic).

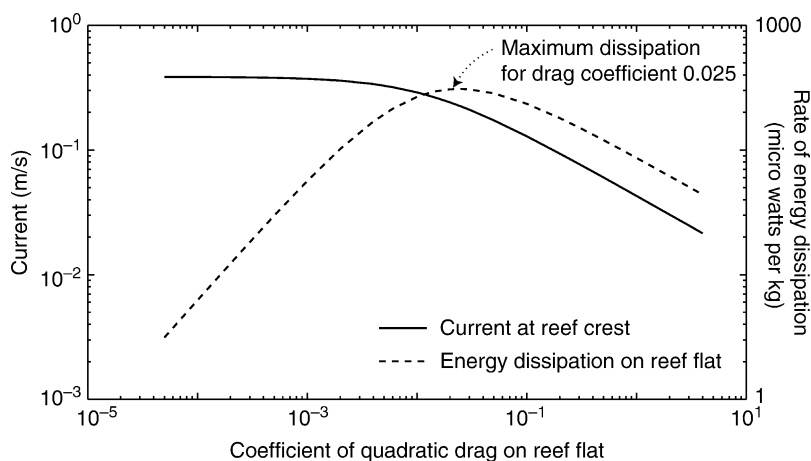
The dynamical force which moves water onto the fore reef is a pressure gradient and this requires a “wave set

down” to be there, just in front of the surf zone which causes water to flow inward towards the surf zone where it must then ascend to the raised water level above the reef crest (Figure 1). It does this by using its own momentum or inertia. The region in front of the surf zone is therefore called the “acceleration zone.” Friction opposes this acceleration and so tends to increase the wave set down. This is illustrated in Figure 1. A major difference between the wave set up, produced by wave breaking, and the wave set down, due to friction, is that the latter increases with current. The wave set down therefore acts as a form of resistance which lowers the net water elevation at the crest when the current over the reef flat would otherwise become too high.

The model used in Figure 1 assumes that the lagoon is sufficiently deep to produce negligible surface elevation immediately behind the reef flat. In practice, most reefs have a “back reef” which is also shallow so that narrow lagoons behind fringing reefs such as Ningaloo (Hearn and Parker, 1988) may experience significant wave set up against the coast behind the lagoon.

### Smooth reef flat

Many reef flats can be quite smooth and this alters the reef hydrodynamics. If we reduce the roughness of the reef flat, we would expect the wave-driven current flow to increase since we would anticipate that the water level at the reef crest remains unchanged. This does occur provided that we do not decrease the roughness of the reef flat too much. As we further lower the roughness of the reef flat, the current increases sufficiently for the wave set down on the fore reef to effectively reduce the elevation at the crest so as to eventually limit the current. At sufficiently low roughness, the current across the reef flat tends towards a constant value and eventually becomes independent of that roughness. Figure 2 shows the current at the reef crest as a function of the coefficient of quadratic friction on the reef flat. This is derived from the simple one-dimensional



**Hydrodynamics of Coral Reef Systems, Figure 2** Current and energy dissipation at the reef crest as a function of the coefficient of quadratic friction on the reef flat.

model of flow across the reef, shown in [Figure 1](#), and based on a traditional quadratic friction law using a coefficient of friction on the fore reef of 0.1. This illustrates the importance of the spatial variability of roughness in a reef system across its many zones.

### Currents around reefs

Currents flow around reefs, as well as over, and through, the actual structure of the reef. As they do so, they create a series of coastal boundary layers near the reef and form island wakes. The structure of these wakes is controlled by the frictional Reynolds number (Hearn, 2008). The high friction, and limited water depth, associated with reefs lowers this Reynolds number and so causes island wakes around these structures (Tomczak, 1988). There are a series of studies of these wakes and the role of friction; for a good review see Wolanski (1994). Local artisan fisheries use their knowledge of these wakes, and whirlpools, around reefs, and their variation with the state of the moon, to navigate these waters and optimize catches (Johannes, 1981).

### Waves on reefs

#### Wave processes

The hydrodynamics of reef systems is closely connected with the processes of wave propagation and breaking on reefs. Waves are present on reef flats whenever there are incoming waves on the fore reef, and in the presence of breaking on the fore reef, the waves on the reef flat are just below the height at which they would break (for example, waves of height 0.8 m on a reef flat of depth 1 m). There are very considerable areas of research devoted to wave breaking and its dependence on the depth and shoaling of the reef and to the effect of the strong wave-current interaction on wave propagation, refraction and diffraction over reefs ("entry Wave refraction"). These processes have many interesting, and distinct, forms on reefs due to their unique structural and hydrodynamic properties.

#### Wave boundary layer

After breaking on the fore-reef, smaller waves (just below breaking height) continue to propagate over the reef flat and these effectively increase friction on the reef flat. In the solid reef model, this wave-current interaction occurs through the "wave boundary layer." The usual situation of waves propagating in the ocean is that their associated currents are not affected significantly by bottom friction. The reason is that the bottom stress is oscillatory and therefore has only the very limited time of half a wave-period to propagate up through the water column. Consequently, until waves enter very shallow water they do not feel significant influences of bottom friction; the vertical current is zero at the bottom of the water column (it is this constraint that changes the speed of propagation of waves in shallow water and produces refraction).

The limited time for propagation of the bottom stress into the water column restricts its influence to a bottom

layer (called the "wave boundary layer"). This layer is very thin in most coastal situations and so it just has the simple effect of increasing the coefficient of quadratic friction through the "wave-current" interaction. This situation is changed on reefs because the greater friction produces considerable turbulence from waves with much greater penetration into the water column. Consequently, the wave boundary layer on reefs can have a thickness comparable to the height of the water column and this effectively increases the roughness of the reef. The usual quadratic friction which we find in most coastal situations is a consequence of the current being responsible for both the generation of turbulence and bottom stress. Within the wave boundary layer, that turbulence is created by the waves. A consequence is that at low currents the bottom frictional stress on the reef can be linearly related to the current. This affects some of the basic hydrodynamics such as the relationship between incoming wave height and current (Hearn, 2008). The current-wave interaction always increases friction; it acts by preventing bottom stress decreasing quadratically at low currents. Parts of the wave boundary layer lie inside the troughs, or cavities, of the roughness elements. These are regions with only marginal penetration by the residual currents from the main part of the water column, and so (depending on their size) some of the cavities may be dominated by wave currents (Lowe et al., 2005a, b).

Wave breaking can produce currents in the order of 1 meter per sec on the reef flat although this is very dependent on the width of the reef flat and its friction. Currents in narrow lagoons behind wave-forced reefs can also be high and especially if there is a deeper trench, or "gully," running through the lagoon. Nearshore reefs parallel to shore ("entry Fringing reef circulation") have breaks in the reef line for water to exit the lagoon ("entry Boat channel"), and during heavy-swell conditions, currents can become extremely high and dangerous to swimmers and novice boaters. Currents on reefs advect and disperse suspended material, and particulate and our knowledge of currents and circulation is vital to an understanding of sediment dynamics and all mass transport ("entry sediment-dynamics").

### Tidal influences

Astronomical tides modulate all of the hydrodynamic processes in a reef system ("entry Tidal effects on coral reefs"). Within the solid reef model, shallow reefs may be completely dry at spring low tides so that the wave set up is confined to the face of the fore reef. In a porous reef model, water continues to have limited flow at these low tides. The overall effect of astronomical tides is to create a net inflow, or outflow (considering all boundaries of the reef system) that is controlled by the tidally varying water level in the reef system. Without the tide, this net flow will be essentially zero. These net tidal currents do depend on the size of the reef system but for small systems the net current is 90 degrees out of phase with the water

elevation. This is based on the water level inside the coral system remaining very close to that in the outside ocean and requires that the size of the system be much less than the distance traveled by a gravity wave in one tidal cycle (this is satisfied by most systems of size a few tens of kilometers).

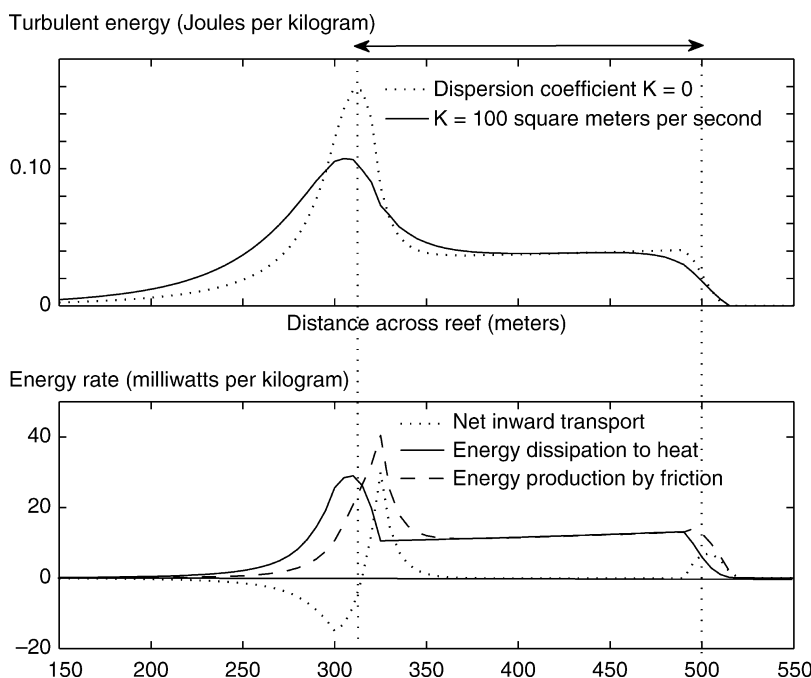
In addition to these “out of phase” tidal currents, time series of water elevation and currents in a reef system, show currents that are “in phase” with the elevation (Kraines et al., 1998). If these are comparable in magnitude to the measured wave driven currents over the reef, it is likely that they are due to the modulation of those currents caused by the changing water level. If the periodic in-phase currents are positively directed over the reef on the rising tide, this means that increasing the water level increases the wave driven current. That may be due to the dilution of the effects of friction with increased height of the water column. Conversely, a decrease in current might be due to reduced wave breaking. This was studied in detail by Hearn (1999) and modeled by Hearn and Atkinson (2000) and is confirmed by measurements at Ningaloo Reef by Hearn and Parker (1988) (“entry Sea level changes and effects on reef growth”).

### Turbulent energy

Friction in reef systems produces turbulent kinetic energy in the water column. The rate of production depends on both friction and current. The simplest physical picture of the turbulence is a set of vortices, or eddies, with continuous

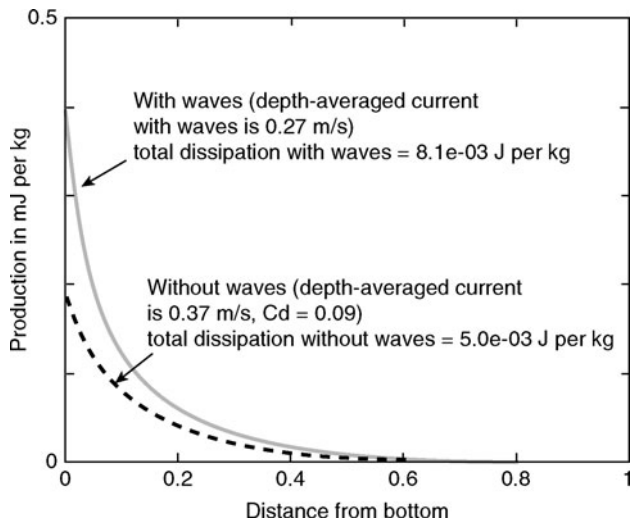
variation of size. It is believed that after kinetic energy enters the turbulence spectrum it cascades down through the vortices, with decreasing spatial scales, until it is dissipated at small scales by molecular viscosity (as heat). Production rates of turbulent energy vary spatially across the reef and are controlled by current strength and roughness (which includes the wave-current interaction). Some part of that energy production is transported to other parts of the reef, where it may dissipate, or leave the reef system, and the remainder is dissipated locally. This balance of turbulence generation by friction, transport of turbulence (by advection and diffusion) and its dissipation, is important to organisms for which biogeochemical and other processes are controlled by some aspect of turbulence. Many organisms, such as coral, have a major role in the development of the roughness elements which promote friction.

Figure 3 shows turbulent energy on the reef which was featured in Figure 1, for the case of a rough reef flat. The upper panel shows the turbulent energy distribution with, and without, the diffusion of turbulence. It shows that diffusion tends to broaden the peak in turbulence at the reef crest. The lower panel shows the rates of production of turbulence, dissipation and net transport which demonstrates that production and dissipation are balanced on spatial scales of meters, over most of the reef, although there is net transport away from the reef crest. A caveat is necessary here regarding the turbulence closure scheme of the model (Hearn, 2008), which is based on conventional coastal models and not yet verified for very rough surfaces. The measurement of production and dissipation in the field are technically



**Hydrodynamics of Coral Reef Systems, Figure 3** Turbulent energy on the reef (featured in Figure 1), for the case of a rough reef flat. The *upper panel* shows the turbulent energy distribution in the absence of diffusion (*broken line*) and with a high diffusion coefficient of  $100 \text{ m}^2 \text{ s}^{-1}$  (*full line*). The lower panel shows the rates of production of turbulence, dissipation and net transport.





**Hydrodynamics of Coral Reef Systems, Figure 4** Rate of turbulent energy production on reef flat (shown in Figure 1) without waves (broken line) and with maximum (just below breaking point) waves.

challenging tasks which were performed at Biosphere 2 in Arizona (Hearn, 2001b), Kaneohe in Hawaii and the Gulf of Aqaba in the Red Sea (Reidenbach et al., 2006). These measurements generally support the local balance of production and dissipation; the values for dissipation are based on the spectral use of the “inertial subrange” for turbulence (Hearn, 2010).

Turbulence production is increased by wave motion, especially at the bottom of the water column and Figure 4 illustrates the effects of maximum waves (just below breaking point) on turbulence production on the reef flat. The figure shows production with, and without, waves. In the absence of waves, the depth averaged current is  $0.37 \text{ ms}^{-1}$  (drag coefficient 0.09), giving a total production of  $5.0 \text{ mJ kg}^{-1}$ . With waves, the current drops to  $0.27 \text{ ms}^{-1}$  but production increases to  $8.1 \text{ mJ kg}^{-1}$ . We note that waves reduce the residual current but, through their effect on friction, increase turbulence production (and therefore dissipation).

Returning to Figure 2, the broken curve shows the rate of energy dissipation at the reef crest as a function of the coefficient of friction on the reef flat (with a fore reef of fixed roughness). Significantly, this shows there is an optimum value of the coefficient of friction on the reef flat that optimizes dissipation and therefore would provide maximum nutrient uptake rates within the dissipation-uptake law (Baird et al., 2004). Importantly, increasing roughness does not necessarily increase dissipation because the spatial variability of roughness is always an important control of hydrodynamic processes.

### Flushing times of reef systems

Flushing times, or residence times, of reef systems are controlled by advection and dispersion (“entry Residence

time”). Flushing processes resemble those in other coastal systems (Hearn, 2008) except that reefs have topographic complexity, high friction and turbulence, with strong wave induced advection (Kraines et al., 1998). Flushing times are defined for the whole reef system, or a sub-system (control volume). They are very dependent on the spatial scale of this subsystem. There are important issues as to the relative strengths of advection and diffusion (dispersion) which are dependent on spatial scale and have important consequences for the transport of many materials and the ecological dynamics of the reef.

Consider particles that are carried onto the reef from the surrounding ocean and have a volume concentration of  $C$  in the water column. If there is a sink for these particles on the reef, its strength can be represented by  $-\gamma C$  where  $\gamma$  has the dimensions of speed. Suppose  $h$  is the depth of the reef and  $u$  a typical current strength. In the absence of dispersion, the characteristic horizontal length,  $l$ , over which the sink affects the concentration  $C$  is  $uh/\gamma$ . Typical values of  $\gamma$ ,  $h$  and  $u$  are  $10^{-4} \text{ ms}^{-1}$ , 1 m and  $0.1\text{--}1 \text{ ms}^{-1}$ , respectively, so that  $l$  is of order 1–10 km. For dispersion

alone, the corresponding distance is  $\sqrt{hK_x^3/4\gamma}$  where  $K_x$  is the coefficient of horizontal dispersion, and so for a typical range of  $K_x = 1\text{--}10 \text{ m}^2 \text{ s}^{-1}$ ,  $l$  is of the order 50–1,500 m. This implies that reefs with currents  $u$  of the order  $1 \text{ ms}^{-1}$  are dominated by advection whereas dispersion can be more important to the transport process when  $u$  is of the order  $0.1 \text{ ms}^{-1}$ . We may also be interested in particles that are produced on the reef, and which have (ideally) zero concentration in the outside ocean. Particles drift downstream and diffuse laterally with a half-width of  $\sqrt{2xx_K}$  where  $x$  is distance from the point source and  $x_K$  is the characteristic distance  $K_x/u$ . Since  $x_K$  is typically 1–100 m so that over a typical reef width of 500 m, the plume will have a half width of 30–300 m depending on the dispersion coefficient and the advective speed.

These results may also be applied to subsystems of the reef using values of residual current and dispersion appropriate to those spatial scales. In some systems, tidal advection dominates flushing and this is important to the dynamics of many larvae (Hamner et al., 2007). A more rigorous approach to finding flushing times is to use the particle-age technique (Hearn, 2006).

### Richardson Plot

The detailed surface area of the individual elements of a reef structure (per unit horizontal planar area of the reef) is of major importance to biogeochemical processes and to the role of hydrodynamics in the ecology of the reef. The surface area, and height, of roughness elements also controls friction which is a prime process in reef hydrodynamics. Surface area is a controlling factor in the surface stress imposed on the reef by currents and waves, and so is important to the constant erosion that occurs on reefs (“entry Solution processes/erosion”) and especially to storm damage from extreme currents and waves (“entry Tropical cyclone/hurricane”).

One of the key theoretical tools used to study these structural aspects of reefs is the “Richardson plot” (Hearn, 2008). This is based on the length,  $S$ , of a chain which is composed of links of size  $s$ , and made to fit, as tightly as possible, over the surface of a reef between two points on the reef with a straight-line (not necessarily horizontal) separation  $s_0$ . The maximum link size that we could choose is evidently  $s_0$ . Experiments with chains are widely used on reefs (e.g., Purkis and Kohler, 2008) and we can also emulate these field experiments with numerical procedures if we have data on the three-dimensional structure of a reef. Numerically, we can also repeat the chain experiment using a net with individual mesh elements each having a surface area of  $s$ , fitted tightly over the reef, and compare the total area of the net,  $S$ , with the flat projection of that area  $s_0$ . These procedures give the linear (or areal) “rugosity”  $S/s_0$  from scale  $s_0$  to  $s$ . The decadal rugosity  $r_{10}$  refers to the case  $s_0/s = 10$ .

The Richardson plot is dependent on the position on the reef that we choose for our chain, or net, and will differ greatly between the various zones of the reef. So, we think of the rugosity as a strictly local measure. We can increase the length of the chain, or the total area of the net, until we cover the entire reef. As we increase the value of  $s_0$ , in this way, we span a larger part of the reef and so  $S(s)$  represents an average over an increasing length, or area, of the reef. In so doing, we do lose strictly local information through this averaging process.

Hydrodynamic models, whether conceptual, analytic, or numerical, use some sort of spatial network of cells which can have a variety of shapes which may not necessarily be the same for all cells. A bathymetry of the reef can be defined at the centers of these cells and this would be the basis of a solid reef model. We can, in principle, make a Richardson plot within each cell with  $s_0$  spanning that cell so that  $S(s)$  represents the cell’s “individual topography” within a larger scale “bathymetry” of resolution  $s_0$ .

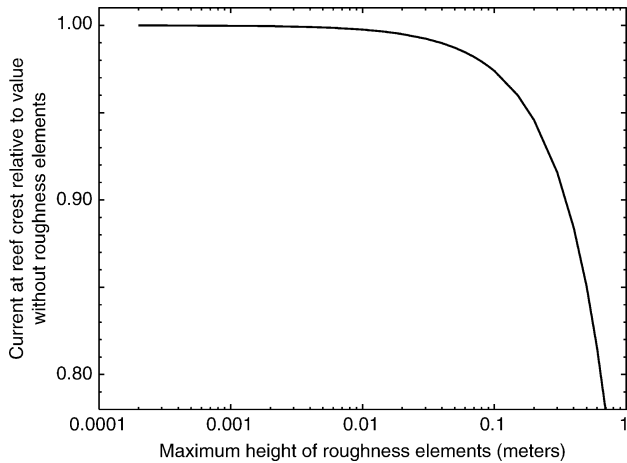
The “dimensional roughness”  $\sigma$  from scale  $s_0$  to  $s$ , is defined as  $\log_{10}(r_{10})$ , or as the mean negative slope of  $\log(S)$  against  $\log(s)$ . It provides a “filling factor,”  $0 < \sigma < 1$  for the reef structure at scale  $s$  within the space defined by  $s_0$ . As an example, a line can be made to completely “fill” a two dimensional space. This is called a “Peano curve” after Giuseppe Peano (1858–1932). The length of a chain fitted over such a line doubles whenever we half the length of its individual links so that  $\sigma = 1$ . Values of  $\sigma$  at scales of 10–100 m for many coastal structures are of order 0.1–0.3, i.e.,  $r_{10} = 1.3$ –2.0. At scales from a few meters to kilometers, filling factors,  $\sigma$ , for reefs of at least 50% ( $r_{10} > 3.2$ ) are reported by Purkis and Kohler (2008) using Lidar data (“entry roughness”). Note that if  $\sigma$  approached unity at  $s = 10$  m, any “holes” in the structure would have a size less than 10 m. Increasing the filling factor increases the surface area and so assists the geochemical processes but does increase the friction and impede flow; it also increases stress, erosion and severity of storm damage.

Rugosity of natural surfaces tends to increase indefinitely as we reduce the spatial scale and this marks their

fundamental difference from geometric surfaces. For example, a geometric surface formed from a flat bottom covered with hemispheres fitted tightly together (so that it looks rather like the back of one of the preformed sheets, or boxes, used to pack hens’ eggs) is a geometric surface and has a limiting areal rugosity (at all spatial scales less than the diameters of the hemispheres) of  $1 + \pi \sim 4$  (relative to a flat plane). This limiting rugosity is otherwise independent of the diameter of the hemispheres. By contrast, natural surfaces do not reach a limiting rugosity at small scales although they may have distinct zones, or ranges, of spatial scales in which limits are effectively reached. In reality, our “egg box” example shows the same phenomenon since at small enough spatial scales we start to see an increase in surface area due to the small-scale structure of the actual material used in its construction. In the same way, most coastal systems are represented by a bathymetry, or topography, which represents the system down to scales of meters. There is then a separation of scales until we see variability at scales that represent sand ripples and sand grains. For these cases, the Richardson plot naturally divides into distinct regions on the  $s$  axis and the important hydrodynamic lengths correspond to values of  $s$  that separate these regions. For example, the roughness lengths used in most coastal systems is the scale at which sand ripples, or sand grains, start to change the Richardson plot. This separation of scales is important to the structure of hydrodynamic processes.

Topography complexity in reefs stretches from scales of 100’s of meters down to millimeters. One very important question is whether there are changes in the Richardson plot which allow some separation of scales. This is likely to occur at the size of individual coral colonies. This scale varies with position in the reef. The basic approach used by Hearn (2010) is to devise an unstructured spatial grid in which one colony occurs in each cell of the grid and cells do not span parts of colonies. Solid reef models incorporate high levels of rugosity at the sub-grid cell scales through increased values of the roughness length. Although simple intuitive estimates can be made of roughness lengths for experimental models, the best approach is to fit the Richardson plot inside a cell to a model of the roughness elements. This involves the form of  $S(s)$  averaged over a numerical cell ( $s_0$  = planar area of cell) with minimum  $s$  one to two orders of magnitude smaller than  $s_0$ . Critical to this fitting procedure is the spatial scales at which the roughness elements start to affect the Richardson plot. For, example, data for individual polyps have been obtained by magnetic resonance imaging from scales of hundreds of microns to centimeters (Zawada et al., 2006).

The Richardson plot for a linear chain can be used to probe the anisotropy of the reef structure. Anisotropy exists in “spur and grove” structures and is common on the windward side of reefs as part of the wave dissipation processes (“entry Spur and groove”). This is important to hydrodynamic processes and is accommodated either by using anisotropic friction or spatially resolving the structure within the bathymetry mesh.



**Hydrodynamics of Coral Reef Systems, Figure 5** Variation of current across reef flat shown in Figure 1 as a function of the height of roughness elements.

Both solid, and porous, reef models use roughness as part of the structural form of the model and require the model to incorporate some skin friction, i.e., conventional surface friction, and so retain a nominal separation of scales between form and skin friction. An example of this methodology is shown in Figure 5 which is based on the reef illustrated in Figure 1. Roughness elements have been built on the reef flat which has a depth 1 m and itself has quadratic skin friction. The model uses cells of a size of 1 m and within each cell there is a randomly chosen height for a roughness element with a maximum height that is varied in the figure from 0.1 to 700 mm. The figure shows that a reduction of current on the reef flat starts to occur for elements of a height of 10 mm and currents decrease rapidly once the height exceeds 100 mm which is 10% of the height of the water column. The model derives the balance of skin friction, inertia, i.e., momentum advection, and pressure gradient around the roughness elements which constitutes form drag. As with classical experiments in fluid dynamics, some skin friction helps to reduce form drag and prevent separation of the viscous boundary layer (Hearn, 2008). The dominance of friction due to roughness elements, over local skin drag, has been verified by Reidenbach et al. (2006) working in the Red Sea. Drag coefficients were measured via the bottom stress obtained from Acoustic Doppler Velocimeters. It was verified that covering the reef flat with plastic sheets did not significantly change these drag coefficients. So, while some skin drag is important, the friction that we find on reefs comes principally from the larger scale roughness.

### Porous reef models

The alternative to the solid reef, or bathymetric, picture of a reef is to treat the reef as a submerged porous system so that water can either pass over the reef or essentially percolate through the structure as in hydrological systems.

The porosity parameter  $p = 1 - \sigma$ , with range  $0 < p(s) < 1$ , effectively defines the “openness” of the reef structure at scale  $s$ . It is also evident that some fore reefs, and reef flats, have structures that contain flow paths that are essentially internal to the reef matrix and have direct surface expression only at the ends of the paths. Measurements of porous flow through reefs are limited. Possible techniques within bore holes have been successfully explored on the Great Barrier Reef by Oberdorfer and Buddemier (1986), on Davies Reef, and by Parnell (1986), on a fringing reef flat at Orpheus Island. They found flow through the reef to be fast although spatially inhomogeneous (Hopley et al., 2007).

Work on porous models is still at very early stages. A major part of the difficulty is measuring the three-dimensional structure of reefs. Optical (Brock et al., 2004) and multi-beam sonar measurements of water depth are providing adequate bathymetry data for solid reef models but do not probe reentrant surfaces of the structure. As such, they determine only “external porosity,” or “external roughness.” Furthermore, it is important to distinguish, and explore, individual colonies and reef structures (Kuffner et al., 2007). Construction of a porous reef model can be attempted from a knowledge of the variation of dimensional roughness  $\sigma(s)$  with scale  $s$ . Some limited experimental progress has been made (e.g., Lowe et al., 2008) with artificial reef communities built as very low canopies on the floor of flumes. These experiments are very similar to those conducted with artificial submerged aquatic vegetation (Nepf and Vivoni, 2000) but lack much of the vertical and topographic complexity, of natural systems, which are essential ingredients of their hydrodynamics.

Simple models of reef growth can be devised with “diffusion limited aggregation.” Simple codes are given by Hearn (2008) and much more detailed algorithms by Kaandorp and Kübler (2001). These are also valuable for experimental modeling of hydrodynamic processes such as the lattice Boltzmann method which is a class of “computational fluid dynamics” (CFD) techniques for modeling a wide variety of complex fluid flow problems with complex boundaries (Succi, 2001).

### Summary

The science of water flow in coral reef systems is a developing area of study and one that is important to much of our understanding of coral reefs. Data on physical processes on reefs is accumulating but still sparse. Much progress is being made in understanding, and measuring, the topographic complexity of reefs. Some of the consequences of that complexity are the nature of friction on reefs and the ways that it can be parameterized. More structural data is needed at spatial scales of meters to centimeters. One of the important properties of reefs that dominates much of reef hydrodynamics is the spatial variability of friction. Considerable progress is being made with models of reef hydrodynamics and our understanding of the roughness and wave boundary layers.



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### Cross-references

[Boat Channel](#)  
[Fore Reef/Reef Front](#)  
[Fringing Reef Circulation](#)  
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[Reef Structure](#)  
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[Waves and Wave-Driven Currents](#)  
[Wave Set-Up](#)

## IMPACTS OF SEDIMENT ON CORAL REEFS

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### Introduction

The relationship between reefs and sediments has been observed by humans certainly for centuries, and possibly for millennia. Columbus observed that his ships could take on fresh water by avoiding the fringing reefs of South America and sailing into the mouths of the Orinoco (Morison, 1974). Moreover, that keen observer Charles Darwin noted that “The deposition. . . of sediment, checks the growth of coral-reefs” (Darwin, 1842).

Since the earliest seafarers noted that they could approach reef-barred coastlines at river mouths, because no reefs occurred there, we have known that sedimentation kills reefs. In fact, throughout geologic history (including the present), sediment must be considered one of the great killers of reefs. Notwithstanding this, the field still lacks the definitive body of research that would allow management teams to set objective standards and to craft appropriate legislation.

### A geological perspective

A great deal of research has been conducted by geologists on coral reefs because of the hydrocarbon resources located within ancient reefs. The framework of these ancient reefs was produced by a wide variety of types of invertebrates, as well as corals with algae, brachiopods, crinoids, and mollusks included in the mix. Many ancient reefs are seen, whether in core or in outcrop, to be covered

by a shale unit, and the assumption has been made that the reefs were killed by sediment input. The immediate cause of the demise was not as important to the geologist as was the fact of the shale-capping unit, because that often transformed the porous reef unit into a hydrocarbon reservoir. Adams and Frenzel (1950), for example, attributed much of the alternating reef facies in the Permian Capitan Reef of West Texas to periodic death of individual reef units from sediment input. Kershaw (1998) describes the complex interplay between morphology and sediment input in ancient stromatoporoid reefs.

In the past few decades, however, further research has afforded more light on the possible/probable causes of reef demise in the fossil record. Hallock and Schlager (1986) suggested that the death of the entire reef tracts could be due to increased surface productivity, driven in turn by increases in nutrients. In the fossil record, increased nutrients can result from increased rainfall, changes in current patterns so as to increase upwelling, or changes in sea level. In today's oceans, of course, increased nutrients are almost invariably the result of human activity. Although reefs have faced sediment stress since their inception, there is evidence that the threat is increasing due to human activities (Fabricius, 2005). Globally, fluvial sediment delivery to the world's oceans is increasing as a result of deforestation and other land clearing for agriculture, although this increase is countered in many watersheds by sediment trapping behind dams (Syvitski et al., 2005).

Hallock and Schlager discuss the changes in reef structure and reef sediments caused by increasing nutrients, and suggest that this process could be linked to the demise of fossil and modern reefs. Their paper functions as a framework, against which various hypotheses for reef decline may be tested. This is also one of the few papers in the past two decades treating reefs as a whole that gives proper place to the critical role of bioerosion in the balance



between reef accretion and reef destruction. In fact, they state (p. 389) "Because rates of carbonate production and bioerosion are similar, even modest increases in nutrient availability can shift a reef community from net production to net erosion." Their treatment of the role of nutrients emphasizes light penetration, and its subsequent diminution by phytoplankton blooms that are driven by nutrient increases. With increasing input from runoff, they envisage a "halo" of nutrients that precede the (usually siliciclastic) sediment input that impacts reef biota, so that by the time the reef is buried by sediment it is already dead or dying.

It is this unholy duo of reef stress, the inextricable linking of sediment input and nutrient increase, that has made the field such a difficult area of research.

That is not to deny the profound, fundamental effect sediment supply and type has on reef development. Roberts and Murray (1983) describe extensive carbonate bank development off the coastline of Nicaragua, an area, which receives copious amounts of rainfall and terrigenous sediment: 3 times more fresh water and 15 times more sediment are introduced per unit length of coastline than on the east coast of the USA. There is an inner smooth-bottomed ramp of siliciclastic sediments parallel to the coast: transition to *Halimeda*-rich bottom sediments is abrupt, and takes place approximately 20 km off the coast. In general, the frequency and proliferation of reefs increase away from the turbid coastal boundary layer and toward the cooler and saltier water that upwells at the shelf margin. But again, nutrients cannot be excluded from the picture. The lack of reefs along the Nicaraguan Rise is at least partly attributed to nutrient increase driven by topographic upwelling (Hallock, 2001).

Acevedo et al. (1989), working in Puerto Rico, reported that increasing coastal development near Ponce, on the south coast, had caused an increase in turbidity, manifesting itself as a plume of sediment-laden water that drifted to the west over a series of reefs. Their survey work showed that total coral cover and diversity was reduced near the sediment source. The surviving corals were sediment-resistant. The effects of the sediment included partial or total burial of corals, bleaching, and colonization of the surface by filamentous cyanobacteria. Reduced light levels resulted in domination of the remaining coral community by species normally found at greater depths—findings similar to those of Cortes and Risk (1985).

Descriptions from the Indo-Pacific of the effects of sediments on modern reefs are equally abundant, and equally well established (Marshall and Orr, 1931). There are descriptions of the effects of mining (Chansang et al., 1981), as well as outlines of the general impact of sediments from activities such as dredging and increased runoff (Endean, 1976; Johannes, 1975; Fabricius, 2005).

## Demonstrated effects of sediments on reefs

### Decrease in coral growth rates

There have been many studies linking decreases in coral growth rates with increased sediment stress, usually from

disturbances such as dredging and deforestation. Bak (1978) found calcification rates decreased by 33%; Dodge and Brass (1984) reported that corals from sites on reefs of St. Croix, US Virgin Islands that had been disturbed by dredging had lower extension and calcification rates than corals from unaffected reefs. Dodge and Vaisnys (1977) found that the growth rate of *Montastrea annularis* in Jamaica decreased as a function of sediment resuspension rates; interestingly, Cortes and Risk (1985) studied the same species in Costa Rica. Their reported resuspension rates were much higher than Dodge and Vaisnys (1977), but produced the same linear relationship. This suggests that coral species have the same responses to sedimentation in different locations.

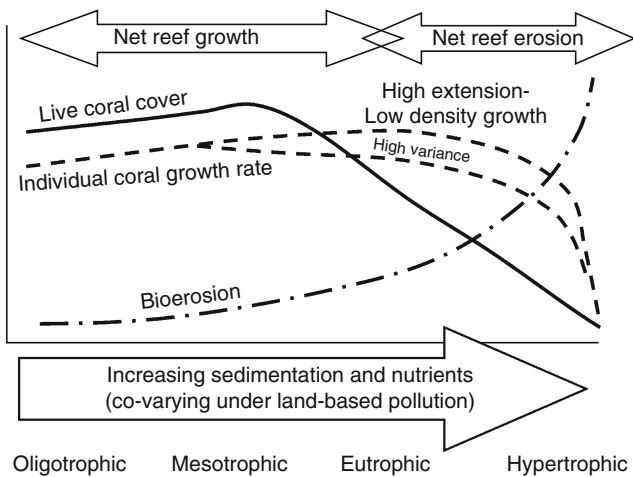
Tomascik and Sander (1985) investigated the effects of water quality on *M. annularis* growth rates off Barbados over a gradient of increasing eutrophication (primary sewage, industrial effluent). They found that mean concentration of suspended particulate matter ( $\text{mg l}^{-1}$ ) was the strongest single estimator of growth rates, with the most rapid coral growth occurring at the site farthest from the primary pollution source.

On the other hand, there is differential species response to similar sediment loadings. Large colonies, and/or species with thick tissues, are often relatively resistant, whereas smaller colonies, and species with thin tissue layers may be greatly affected (Rogers, 1990; Stafford-Smith, 1993; Fabricius, 2005).

Care must be taken when interpreting growth rates reported in the literature, especially in older articles. Coral "growth rate" is not simply linear extension, but should be seen as calcification rate, the rate at which corals can make skeleton. This is the product of both extension rate and density, and it must be noted here that Brown et al. (1990), saw no detectable decrease in coral calcification as a result of dredging.

Because sediment input and nutrient concentration frequently (usually) covary, corals are affected by two conflicting factors: increased sediment input slows growth, while at the same time individual corals may grow faster under conditions of elevated nutrients. These same corals will then face intense competition from algae and non-calcified benthos, and bioerosion soon outstrips accretion rates. This bifold effect of nutrients on coral reefs has been called the "Janus Effect," after the two-faced god of Roman mythology so familiar to theatre-goers (Edinger and Risk, 1994).

Edinger et al. (2000b), working in Indonesia, were able to tease apart the conflicting influences of nutrients and sediment stress. *Porites lobata* coral extension rates increased from oligotrophic to mesotrophic conditions, then decreased again toward eutrophic and hypertrophic conditions as turbidity from sediments and phytoplankton reduced light penetration to corals (Figure 1). High variance in extension rates was observed on polluted Java Sea reefs. They found that extension rates on polluted nearshore reefs were high, and could not be statistically distinguished from extension rates from cleaner offshore reefs, not



**Impacts of Sediment on Coral Reefs, Figure 1** Diagram of the effects of increasing sediment and nutrient input from land, on the carbonate balance of reefs. Modified from Edinger et al. (2000b).

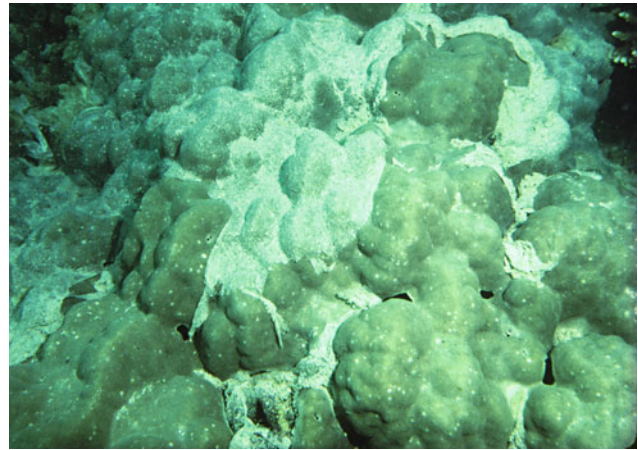
affected by sediments. Among reefs impacted by combined sedimentation and eutrophication, only one of five reefs showed a decrease in average coral linear extension rates through time. Coral skeletal density in nearshore, polluted environments, however, was significantly lower. Low density, high-extension skeletal growth may be a sclerochronological signal of combined sedimentation and eutrophication effects on corals. One of the key conclusions of Edinger et al. (2000b) was that coral growth rates may be a poor indicator of whole-reef health, given the conflicting effects of covarying sediments and nutrients.

#### Partial or total mortality

Death of all or a part of coral colonies has been associated with purported sediment stress. Marszalek (1981) reported partial mortality, accompanied by copious mucus secretion by the corals. Many corals secrete mucus when stressed by sediments; evidently as a defense, the mucus is shed off the colony, carrying with it the trapped sediment (Figure 2). In a series of papers, Bak and coauthors (Bak, 1978, 1983; Bak and Steward-van Es, 1980) outlined a series of experiments and observations linking partial coral mortality to external stress. In their work in Thailand on the impacts of dredging, Brown et al. (1990) described partial coral mortality, accompanied by mucus secretions. Nugues and Roberts (2003) described partial mortality on corals in St. Lucia, and suggested that a measure of partial mortality may be used as an indicator of sediment stress.

#### Decrease in metabolic rate

Rogers (1979) shaded a portion of San Cristobal reef (Puerto Rico) to simulate the shading effects of turbidity and found decreased net productivity by the coral community. Dallmeyer et al. (1982) found a decrease in net production by *M. annularis* colonies exposed to particulate



**Impacts of Sediment on Coral Reefs, Figure 2** Fine carbonate sediment bound into a mucus sheet on a colony of *Porites*, Zanzibar, East Africa. This coral also exhibits the multilobate morphology believed to result from sediment stress.

peat during daytime experiments. At night, colonies exhibited increased respiration and active clearing behavior. Telesnicki and Goldberg (1995) found that high turbidity increased mucus production, and depressed P:R ratio to below 1.0.

More recently, Philipp and Fabricius (2003) assessed the effect of sediment stress by using PAM fluorometry on field and laboratory experiments on the Great Barrier Reef. Within the ranges measured, sedimentation stress of colonies exposed to large amounts of sediment for short periods of time was similar to that exposed to low amounts of sediments for prolonged periods of time. Colonies recovered from short-term sedimentation stress within <36 h, whereas long-term exposure, or high levels of sedimentation, killed exposed colony parts.

#### Changes in coral population structure

Several authors have observed that one of the effects of sediment stress appears to be a replacement of shallow-water species by species characteristic of, or adapted to, deeper reef zones (Cortes and Risk, 1985; Acevedo and Morelock, 1988). Rogers (1990) suggested that heavy sediment stress should result in an upward shift in depth zonation.

It has also been suggested that, as a consequence of reduced recruitment on heavily sedimented reefs, the population structure of the surviving coral will shift toward a preponderance of large, old colonies. At Cahuita, Costa Rica, Cortes and Risk (1984) found a correlation of heavy river discharge with lower diversity, lower cover, lower growth rates, and generally larger coral colonies. Maragos (1974) also found larger colonies in the turbid lagoon than in the clear lagoon at Fanning Island.

#### Changes in coral morphology

Colonies of *Agaricia agaricites* and *M. annularis* exhibited changes in orientation and morphology, which

appear to reflect adaptations to sediment stress (Bak and Elgershuizen, 1976). Logan (1988) suggested that the frequently observed orientation of the large calyx in *Scolymia cubensis* at a steep angle from the horizontal may be an adaptation, which facilitates sediment removal. Under high sedimentation conditions, massive coral colonies often take on a multilobate morphology, which allows the coral colony to continue extending upward in some portions, while other portions of the colony grow slowly or die altogether.

### Reduced species richness and diversity

A reduction in the number of species of coral, coral cover, and the diversity of the coral assemblage seems to be virtually universal results of sediment stress. Such results have been reported by many authors, and only a few examples can be given here: Caribbean-Costa Rica, Cortes and Risk (1985); Puerto Rico, Acevedo and Morelock (1988); Virgin Islands, Rogers (1983); Bermuda, Dryer and Logan (1978); Indian Ocean-Kenya, Obura et al. (2000); Arabian Gulf, Sheppard et al. (2000); Madagascar, Gabri   et al. (2000).

It is perhaps in Southeast Asia, where major rivers, abundant reefs, impoverished coastal populations, and rampant development all converge, that perhaps the most depressing examples of sediment-driven reef degradation may be found: Philippines, Hodgson and Dixon (1988); Singapore, Chou (1997), Dikou and van Woesik (2006); Thailand, Chansang et al. (1981).

Indonesia has more coral reefs than any other nation, and also some of the most badly damaged reefs. Edinger et al. (1998) described the trajectories of decline of reefs from several areas near Java, Sulawesi, and Ambon (Moluccas), and outline the impacts on diversity from sediments, nutrients, and direct human impacts such as anchor damage. Combined sedimentation and eutrophication caused greater change in species composition than either factor alone, or than mechanically induced stresses such as blast fishing or anchor damage (Edinger et al., 2000a). Science writing is supposed to be dry and objective, yet it is hard to read the description, by Tomascik et al. (1994), of the decline of the reefs in Jakarta Bay without feeling it is a modern tragedy. They quote Umbgrove (1939), writing about the reefs of Nyamuk Besar ("Big Mosquito" in Bahasa Indonesia; Leiden, to the Dutch residents): "The unrivaled splendor and wealth of forms and the delicate tints of the coral structures, the brilliant colors of fishes, clams, sea anemones, worms, crabs, star fishes and the whole rest of the reef animals are so attractive and interesting that it seems impossible to give an adequate description of such a profusion of serene and fascinating beauty."

Those reefs have now disappeared. Tomascik et al. describe the disappearance of entire reef tracts in Jakarta Bay and the adjacent ocean waters, driven by the onslaught of sediments and nutrients from the city. They go on to say (p. 309): "Jakarta Bay is not an isolated case of reef degradation, which is now a worldwide phenomenon. . . monitoring. . . will not prevent the demise of coastal

reef ecosystems, but ecologically sound management practices and coastal development based on sustainable principles just might."

### Reduced larval settlement

As might be expected, the early stages of coral development, the processes of larval settlement and development, are strongly affected by sediment in the water column. Tomascik and Sander (1987) suggested that lower light levels may inhibit development of coral larvae by reducing the amount of energy available to maturing ova or embryos. They found reduced numbers of larvae from colonies of *P. porites* growing on reefs polluted by nutrients and suspended particulate matter with increasing levels of sedimentation and eutrophication.

Sedimentation mortality thresholds for coral recruits are an order of magnitude lower than those for larger colonies (Fabricius et al., 2003). Few coral larvae settle on sediment-covered surfaces, and survival on such surfaces is minimal. At moderate to high rates of sedimentation, successful larval settlement is restricted to downward-facing surfaces where growth and survival are negatively affected by low light.

In short, there is a long list of perceived impacts on corals that have been attributed to the effects of sediments. At present, however, these are impacts in search of mechanisms. The field requires more research on the specific modes of action, by which sediment stress achieves the observed results.

### Mode of action of sediments

There are basically three avenues that have been suggested and by which sediments can stress corals:

#### Decreasing the available light

The logic behind this hypothesis is that decreased light levels would reduce the amount of energy translocated from the zooxanthellae to the host, resulting in slower growth. Rogers (1979) shaded corals in the field, and observed partial mortality. Several other authors have also observed the decrease in coral vigor, which may be produced by decreased light levels (Telesnicki and Goldberg, 1995; Anthony and Hoegh-Guldberg, 2004). Furthermore, fine-grained siliciclastic sediments reduce light penetration more than equivalent concentrations of carbonate sediments (Te, 1997).

#### Metabolic drain

When sediments land on corals, the corals usually try to clean themselves by ciliary action, tentacle waving, or mucus sheet secretion. These responses on the part of the coral suggest that there is a metabolic cost to the corals involved in sediment deposition (Telesnicki and Goldberg, 1995). Corals have a variety of mechanisms for coping with sediments including use of their tentacles and cilia, stomodeal distension through uptake of water, and entanglement of particles in mucus, which later sloughs



off the colony surface (Hubbard and Pocock, 1972). Corals exhibit both active and passive removal of sediment particles (Lasker, 1980). In coral colonies, sedimentation stress increases linearly with the duration and amount of sedimentation: for example, a certain amount of sediment deposited on the coral for one time unit exerts the same measurable photophysiological stress as twice the amount deposited for half the time (Philipp and Fabricius, 2003).

### Microbially mediated decline

This is a relatively recent concept, that links together the co-occurrence of sediment input, dissolved organic matter (DOM), and nutrient increases, such as would accompany river discharge (either normal, or augmented by human activities such as deforestation) with increased bacterial activity. The augmented microbial processes would then increase the virulence of disease, alter the dynamics of fine sediments, and kill corals directly.

Much of the earlier work on sediments and corals paid little attention to the mineralogy and the size distribution of the sediments. This bears further investigation, because mineralogy plays an important role in the potential delivery of toxic and/or deleterious substances to the corals. For example, the phyllosilicate lattices of clay minerals, which will be delivered from the weathering of silicate rocks, are capable of storing (and later releasing) enormous amounts of dissolved substances, trace metals, and contaminants. Because of the edge charges on the unit cells, clay minerals can also form aggregates, or flocs; this tendency is enhanced in the presence of organic matter. Fine-grained carbonate sediments (micrites) lack this storage and agglomeration capabilities; hence, siliciclastic sediments can be predicted as posing greater threats to corals than the same amount of carbonate sediment (cf. Te, 1997).

Impacts of sediments on corals are strongly influenced by the type of sediment. Tissue damage under a layer of sediment increases with increasing organic content and bacterial activity, and with decreasing grain sizes (Hodgson, 1990; Weber et al., 2006). Low levels of sedimentation, when combined with “marine snow,” killed newly settled coral recruits. The same amount of sediment without the addition of marine snow does not reduce their short-term survival (Fabricius et al., 2003). Kline et al. (2006) have shown that increased DOM can cause elevated bacterial activity, leading directly to coral death.

As an example of the sort of research that is needed in this field, Weber et al. (2006) studied the effects on corals of sediments differing in grain size, organic content, and geochemistry. They found that different sediments exerted greatly contrasting levels of stress in the corals, and that grain size and organic and nutrient-related sediment properties are key factors determining sedimentation stress in corals after short-term exposure. Photophysiological stress was measurable after 36 h of exposure to most of the silt-sized sediments, and coral recovery was incomplete after 48–96 h recovery time. In contrast, sandy sediment types caused no measurable stress at the same

concentration for the same exposure time. Stress levels were strongly related to the content of organic matter and nutrients in the sediments. Anoxia developed on the sediment surfaces of the nutrient-rich silts, which had become slimy and smelled of hydrogen sulfide, suggesting increased bacterial activity. Their findings may be summarized as follows: silt-sized and nutrient-rich sediments can stress corals after short exposure, while sandy sediments or nutrient-poor silts have little effect.

### Summary of impacts

In short, the effect of sediments on corals and coral reefs may involve the effect of nutrients and bacteria carried by the sediment plume, as much as the sediments themselves. Although, both shading and particle loading are coral stressors, it would appear that, at least in some cases, shading suppresses coral growth to a greater extent than particle loading per se (Anthony, 1999).

There have been several experimental investigations of the sediment rejecting capabilities of corals (Hubbard and Pocock, 1972; Bak and Elgershuizen, 1976). In addition, in both the Caribbean and the Indo-Pacific, there have been attempts to establish a hierarchy of rejection capabilities among species of corals (Rogers, 1990; Stafford-Smith and Ormond, 1992). Some of the earlier attempts to assess sediment stress have used pulsed loadings of mostly coarse sediment (sand), which bears little relevance to the typical sediment stress applied to corals unremitting muddy water. Some recent research has, however, begun to shed more light on this complex problem (Anthony, 1999; Riegl, 1995). Reefs can, of course, occur in turbid settings. These tend to be thin accumulations, of low diversity, but nonetheless they survive (Perry and Larcombe, 2003). From a management perspective, the important factor is a *change* in water quality.

### Status of research

There is still a great need for research that would establish the limits of acceptable sediment input to any given reef. There may be an indication that Caribbean reefs, at least, cannot for long survive continued levels of SPM (Suspended Particulate Matter) in the surrounding water greater than 10 mg/L (Cortes and Risk, 1985; Abdel-Salam and Porter, 1988), but the certainty of this level is far from established, and legislation based on it is equally far off. In addition, there is a suggestion that some Indo-Pacific reefs flourish at SPM levels much higher, in some cases by shifting their metabolism toward more heterotrophy in murky waters (Anthony, 2000).

There are a number of reasons why research in this field has not progressed as rapidly as perhaps it should. First of all, perhaps the most frustrating, is the inability of workers in the field to agree on common methodology. Sediment deposition rates are usually estimated using sediment traps, but almost every published study uses a different design (trap height, diameter, emplacement above the bottom), and virtually none of them cites Gardner's work on

the proper design of a sediment trap (Gardner, 1980a, b). This is important, because traps with too large a ratio of opening to height will undertrap, whereas those that are taller, with smaller openings, will overtrap. Only traps with the proper design, beginning with a height: diameter ratio of about 3 will produce results that may be compared among sites and locations. In addition, sediment should be removed from the traps every few days, poisoned, and archived. Much of the information in the literature derived from sediment traps, in short, is either undependable or of use only in a limited geographic area. In addition, the material caught in a sediment trap represents both resuspended and net sediment, and these need to be differentiated if a complete picture is to be developed.

There has also been wide divergence in the methods used to measure sediment in the water column, SPM. Engineers and water quality workers have developed instruments, "nephelometers" that basically measure the attenuation of light through a water column as a measure of turbidity. The material in the water, however, may be a richly confusing mixture of alive and dead organic matter, dissolved substances, and sediments of varying grain sizes, colors, and mineralogy. Consequently, a stable synthetic material called "Formazin" with uniform particle size is often used as a standard for calibration and reproducibility. The results are Formazin Turbidity Units, or FTU. In the USA, the EPA has specified a white-light source and certain aspects of the instrument, to obtain Nephelometer Turbidity Units, or NTU.

The main attraction of these measurement techniques is that they are quick and easy, but, like many quick and easy methods, they often come with inherent errors. Because the type of sediment and the proportions of plankton and other organic matter can vary so widely, best practice is to calibrate the nephelometer against actual SPM values at each site and then, of course, the values so attained may not readily be transferred to other sites.

The other method used to determine suspended particulate matter is direct measurement: a known volume of water is filtered through a pre-weighed fine filter (generally 0.45  $\mu$ ), and the filter is dried and weighed (the method is described in Cortes and Risk, 1985). This process takes more time, but provides precise estimates. Perhaps equally important, the filters may be saved for later analysis of mineralogy, micropaleontology, and trace elements.

FTU and NTU should not be used in reef research. The quality of the data so produced is inadequate for research purposes, although the ease of acquiring such data may be attractive. Although NTU have been used by, for example, USEAP to set water quality guidelines, the high SPM values that characterize many reef sites, and the critical importance of being able to identify sediment provenance, mitigates against the instrumental methods in use.

Discussion of sediments in the literature has also suffered from some imprecision. Resuspension rates are not the same as sedimentation rates. From the point of view of the coral, an area with constant resuspension of bottom sediments is just as stressful as net deposition of the same

amount of sediment, yet the two situations represent very different settings. Corals react differently to fine versus coarse sediments – in addition, the textural and chemical properties of sediment are a function, at least in part, of the mineralogy.

Ideally, then, any study of sediment stress on a reef should therefore provide information on sediment deposition rates, resuspension rates, and SPM values, as well as data as to grain-size distribution and mineralogy. The number of published articles satisfying these requirements is disappointingly small.

The reasons for this may lie in the fact that much of the literature on the effects of sediment leaves much to be desired. Because coral reefs are a geobiological construct, their study – even more so than other ecosystems – requires a fundamentally interdisciplinary approach. The need for this has been a subject of comment many times (e.g., Risk, 1999), but the tendency still is to a one-dimensional approach.

Not only has some of the previous work on sediment stress been less than ideal, there has been delay in adopting some useful techniques. That corals incorporate sediment into their skeletons has been known for decades (Barnard et al., 1974). Cortes and Risk (1985) used this phenomenon to assess sediment input by decalcifying coral samples and estimating the insoluble residue. True, it only is effective where the incoming sediment is siliciclastic; the high variance encountered in Budd et al. (1993) arise from mixing samples, from sites with predominantly siliciclastic sediments as background input with samples from carbonate terrain. Davies (1992) showed that corals incorporate sediments through micro-lesions in the tissue, which in turn may be caused by sediment stress. Where others have used this technique to assess sediment stress, it has proven to be useful. Macintyre et al. (1994) traced the decline of a *Porites*-dominated reef in Golfo Dulce, Costa Rica, by analyzing the mineralogy of sediments trapped in coral colonies. David (2003) estimated input of heavy metals from mine tailings in the Philippines, and Edinger et al. (2008) traced the impact of gold mining on corals of Sulawesi, Indonesia. Brown et al. (1990) reported the incorporation of iron into coral skeletons in Thailand. Recently, Risk et al. (2009) have suggested that it may be possible to tease out the mixed influences of sediment and nutrients by plotting trapped sediment in coral samples (insoluble residue) against  $\delta^{15}\text{N}$  of the coral tissue; this is an area that needs more work.

The corals themselves also may not cooperate with studies designed to show linear responses to sediment stress. In nature, incoming sediment usually will contain additional nutrients and plankton, so it represents a potential food source as well as a potential stressor. Many coral species are very plastic in their feeding behavior, and have been shown, for example, to shift to a more heterotrophic feeding mode when faced with increased sediment. Anthony (2000) has shown this experimentally, and Risk et al. (1994) have shown that past metabolic shifts are recorded in the isotopic signatures in the skeletons. Similarly, Risk

et al. (1994) and Sammarco and Risk (1999), using stable isotopic tracers of metabolic activity, have shown that near-shore corals of at least some species can obtain much of their nutrition from terrestrial sources. Analysis of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of *P. lobata* coral tissue of Indo-Pacific reefs subject to combined sedimentation and eutrophication showed the influence of both enhanced algal photosynthesis, fueled by increased inorganic nutrient availability, and heterotrophy, fueled by increased dissolved or particulate organic matter availability. The relative enhancement of these different processes, in differing proportions, depends on the relative influences of turbidity, organic matter loading, and inorganic nutrient loading.

Recent research on the fringing reef of Molokai, Hawai'i by the USGS has set the bar for sediment research in coral environments. As a selection from this large body of work, Bothner et al. (2006) employed very sophisticated sediment traps, and were able to conclude that sediment input to the reef was episodic, driven by storms. What is more, sediment traps were found not to be good indicators of net sediment accumulation. Presto et al. (2006) studied the temporal and spatial variability of flow in suspended sediments on the reef flat, and found that most of the sediment was transported alongshore. Regions where sediment moved offshore were regions of low coral cover. Calhoun and Field (2008) studied the composition of grain types from the beaches and reef environments, and were able to deduce transport directions. And finally, much of this research is summarized in the beautifully illustrated USGS report (Field et al., 2008).

### Guidelines – how much sedimentation is too much?

In short, development of an integrated set of guidelines for sediment resistance of reefs has been hampered by lack of agreement on methodology, lack of precision when dealing with the sediments themselves, the confounded effects of increased sediment input and increased nutrients, and the plasticity of coral behavior.

It is highly unlikely that there can ever be one set of regulations, or guidelines, developed for all reefs that could control impacts of sediment (cf. Pastorok and Bilyard, 1985), nor is a global set of water quality guidelines necessarily desirable. It would seem that most Caribbean reefs have difficulty surviving SPM loads that are consistently in excess of 10 mg/L, and indeed it would seem appropriate to incorporate that level into regulatory guidelines. Reefs in other locales, for example, the northern Great Barrier Reef, will have adapted and evolved to survive very different conditions (Hopley et al., 1990, 2007). Corals near the mouth of the Daintree River flourish under conditions that would slay a Caribbean reef (cf. Perry and Larcombe, 2003). Within each region, corals have adapted to long-term regional variation in normal sedimentation rates and patterns. High-ambient sedimentation levels are not inherently stressful; rather, it is the change in the rates of sedimentation that causes stress for coral reefs (Fabricius, 2005; Hopley et al., 2007).

Even recognizing that change in sedimentation rate, rather than absolute sedimentation rate, is crucial for coral reefs (cf. Dikou and van Woesik, 2006), it is unlikely that a single critical value for percentage increase in sedimentation can be identified for all reefs. Sedimentation in many environments is highly episodic, and corals living in areas of high ambient sedimentation can probably tolerate a higher variance in sedimentation rate than those living in clear-water, low-sedimentation settings. It is highly likely that separate guidelines will have to be developed for each reef province, and we are a very long way from being able to produce those guidelines.

### Sclerochronology: the two-edged sword

Sclerochronology is the study of past environmental conditions by way of the study of the records in skeletons; corals and bivalves are the most commonly used. By “two-edged sword” here it is meant that, in many cases, corals are capable of recording the timing and extent of the very stresses that are killing them.

Coral skeletons record the environmental conditions under which the coral has grown, and in particular can provide an annually resolved record of how those conditions have changed through the life of the coral. Variables responding to sediment that can be recorded in coral skeletons include skeletal density, extension and calcification rates, quantity and mineralogy of insoluble residue, stable isotopes of C and O, and trace element geochemistry. Insoluble residue mineralogy and trace element geochemistry are particularly useful for studying the effects of sedimentation on reefs, especially determining the source of sediments. Trace element studies in coral skeletons have been particularly useful in recording sedimentation from natural terrestrial runoff (often enhanced by land clearing for agriculture or forestry), urban runoff including sewage pollution, and mine tailings. The discussion below focuses on trace element analyses of coral skeletons to reflect quantity and type of sedimentation. Trace elements differ in the extent to which they are incorporated into coral skeletons as a function of their valence state and atomic radius. Cations with valence similar to Calcium, such as Strontium and the Lanthanides are most readily incorporated into the aragonite crystal lattice, explaining why Sr/Ca ratios can be consistently recorded in coral skeletons at mmol/mol levels (see Gagan et al., 2000 for review). Ratios of Mg/Ca, Sr/Ca, and U/Ca respond to sea-surface temperature consistently, but with varying sensitivity (Fallon et al., 2003). These elements are useful in sediment studies for chronological control (in seasonal settings) and for records of changing oceanographic conditions at seasonal to decadal time-scales. Trace elements offer advantages over  $\delta^{18}\text{O}$  and fluorescent bands in responding to sea-surface temperature independent of salinity or fluvial discharge, but are most powerful as recorders of climate variation when combined with  $\delta^{18}\text{O}$  (Gagan et al., 2000). Other trace elements reflect natural and anthropogenic sedimentation directly (see below).



Trace elements in coral skeletons can be measured by drilling out samples of coral skeleton, followed by wet chemical analysis using atomic absorption spectrometry (AAS; Khaled et al., 2003), inductively coupled plasma mass spectrometry (ICP-MS; e.g., Fleitmann et al., 2007), or inductively coupled plasma atomic emission spectrometry (ICP-AES; Bastidas and Garcia, 1997; David, 2003). Of these, the standard method recommended by USGS is ICP-AES (see Bastidas and Garcia, 1997; David, 2003). Recent developments in laser-ablation mass spectrometry (LAM-ICPMS) and secondary ion mass spectrometry (SIMS) allow high-resolution sampling of trace elements in coral skeletons without wet chemistry (Sinclair et al., 1998; Fallon et al., 2002, 2003; Rollion-Bard et al., 2003), but function most effectively on elements incorporated directly into the coral skeleton, and may require custom modifications to off-the-shelf analytical systems (Fallon et al., 2003). Incorporation of metals and metalloids into coral skeletons varies as a result of atomic radius – cations with radius similar to that of calcium, such as Ba, Cu, Fe, Pb, Sn, and Zn are most readily incorporated from a dissolved state into the lattice (see Howard and Brown, 1984, for review). Of these, Ba is the best indicator of sedimentation from fluvial sources, and can record spatial and temporal variation in fluvial input far from river mouths, with concentration increasing with proximity to source (Fallon et al., 2003; McCulloch et al., 2003b). Ba/Ca ratios in coral skeletons have documented increased sediment flux to coastal coral reefs through soil erosion associated with agricultural expansion and deforestation (e.g., Anderegg et al., 1997; McCulloch et al., 2003a; Fleitmann et al., 2007). In areas with basaltic soils, soil erosion and sedimentation also results in increased phosphorus delivery to reefs (McCulloch et al., 2003b). Combined with increased anthropogenic nitrogen fixation and delivery to coastal watersheds (Vitousek et al., 1997), this sedimentation is often accompanied by eutrophication.

Chemical analysis of coral skeletons accurately records sedimentation from point or non-point sources containing these metals, such as urban runoff (e.g., Bastidas and Garcia, 1997; Runnalls and Coleman, 2003), offshore oil exploration and production near cold-water coral reefs (e.g., Gass and Roberts, 2006; Lepland and Mortensen, 2008), or some mine tailings, particularly from tin, copper, lead–zinc, and iron mines (e.g., Changsang, 1988; David, 2003), or some gold and silver mines containing aragonite-compatible trace elements.

Other elements, such as Co, Cr, Ni, As, Sb, and Hg are not readily incorporated into the aragonite crystal lattice, and are present in coral skeletons at much lower concentrations, mostly as included sediment particles. These elements, which are often associated with nickel mines or sediment-hosted gold mines, exhibit high spatial variation within coral skeletons, and generally low concentrations in coral skeletons compared to their concentrations in reef sediment (Edinger et al., 2008). Although these elements can be directly measured in coral skeletons using LAM-ICPMS,

spatial variation in concentration including sediment particles within the skeleton requires extensive sampling to integrate over a large area of coral skeleton (e.g.,  $50 \times 500 \mu\text{m}$  mask, Fallon et al., 2002), or drilling of subsamples followed by wet-chemical analysis using ICP-AES.

Corals may then be used to monitor sediment influx, river discharge, industrial activity, and several other types of input. Care needs to be taken in chemical analyses of coral skeletons, because exogenous compounds may either be trapped/bound directly into the skeletal structure, or be part of individual sediment grains trapped within skeletal cavities. Notwithstanding this reservation, the information gathered by such geochemical techniques can be extremely useful. In some cases, the temporal resolution of individual events may be excellent. Heikoop et al. (1996) describe the effects of a short-lived eruption of the volcano Gunung Api (“Fire Mountain”) in May 1988, in the Banda Islands, Eastern Indonesia. The ash fall from the eruption was several centimeters in thickness on the reef. Most of the branching corals were killed. Surviving massive corals preserve a Fe-rich band in their skeletons, as well as ash particles trapped within algal borings at a death-regrowth surface. When cleaved open, these corals reveal a striking red band, parallel to the growth surface (Figure 3). Heikoop et al. (1996, p. 291) state: “These proxy records provide information on short-lived, low magnitude, volcanic events which affect but do not totally devastate marine communities. The continual growth records of corals will preserve these geologically instantaneous signals with much better resolution than the bioturbated sediment record. Moreover, large massive corals



**Impacts of Sediment on Coral Reefs, Figure 3** Fe-rich band in a freshly cleaved *Porites* colony, the moment of discovery, Banda Api Indonesia. This band, sampled in 1992, is a record of the eruption of the volcano Gunung Api in 1988. When freshly exposed, the band was dark, almost black. On exposure to open seawater, it oxidized to a red color within minutes. The band is indicated by an arrow. Sponge borings (upper centre–left) are indicated by an “S,” and abundant bivalve borings near the base by a “B.”

may record several such events. Accordingly, in appropriate settings, the periodicity of relatively minor volcanic events may be established in the fossil record with much greater precision than previously permitted."

### How to identify if a reef is sediment-stressed

Globally, coral reefs are threatened by a plethora of anthropogenic and natural factors, and many reefs face multiple stressors (Hughes and Connell, 1999). Disentangling sedimentation from the other stressors with which it usually co-occurs is quite difficult (Fabricius, 2005). The following factors typically occur on reefs subject to sedimentation, with or without other stressors:

1. High siliciclastic content in reef sediment
2. High insoluble residue content in coral skeletons, particularly open-lattice species like massive *Porites*
3. High Ba/Ca ratio in coral skeletons
4. Low recruitment rates of corals, often resulting in size distributions skewed to large colonies
5. Low species diversity of corals, relative to reference sites in same region
6. Low percentage live coral cover, combined with high cover of dead coral (high mortality index)
7. Predominance of stress-tolerant coral species and growth forms, especially multilobate massive colonies
8. High-extension, low-density skeletal growth

### Summary

Sediment input is one of the great killers of coral reefs. The effect is accentuated, because in most situations the sediment is accompanied by dissolved nutrients and organic matter. In many cases, however, the source and the nature of the stress may be identified using a variety of geochemical techniques.

### Acknowledgments

The senior author performed much of the work for this article whilst in residence as a Temminck Fellow at the Natural History Museum in Leiden, Netherlands.

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## Cross-references

Bioerosion  
 Carbonate Budgets and Reef Framework Accumulation  
 East Indies Triangle of Biodiversity  
 Fringing Reefs  
 Heavy Metal Accumulation in Scleractinian Corals  
 Indonesian Reefs  
 Nutrient Pollution/Eutrophication  
 Oil and Gas Reservoirs and Coral Reefs  
 Sediment Dynamics  
 Sediments, Properties  
 Turbid-Zone and Terrigenous Sediment-Influenced Reefs  
 Volcanic Disturbances and Coral Reefs  
 Western Atlantic/Caribbean, Coral Reefs

## INDIAN OCEAN REEFS

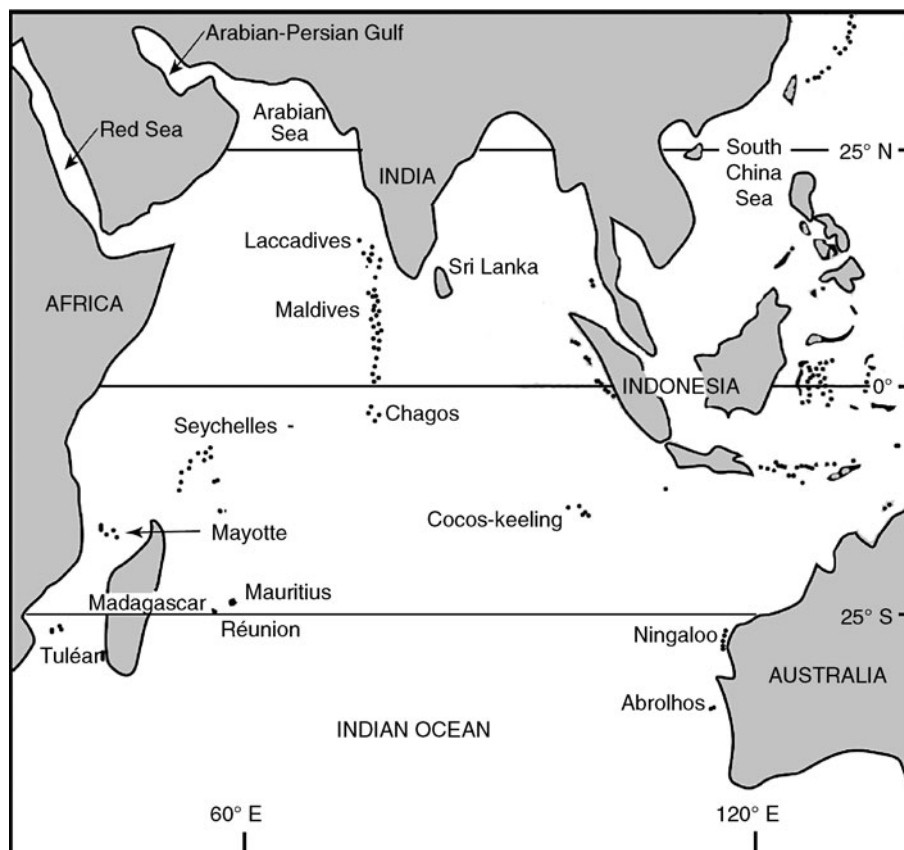
Eberhard Gischler  
 Frankfurt am Main, Germany

### Definition

The Indian Ocean is bounded by East Africa, South Asia, Indonesia, and Western Australia ([Figure 1](#)). It is the world's second largest coral reef province, after the Pacific Ocean.

### Introduction

The Indian Ocean reef area harbors abundant fringing reefs (East Africa and Madagascar region, India, Indonesia, Western Australia) and numerous atolls (Maldives and Chagos archipelagoes, Cocos Keeling). The only well-developed barrier reef is found around Mayotte in the Comoro Islands ([Figure 1](#)). Submerged banks and reefs are common and include Great Chagos, Saya de Malha, Nazareth, and Seychelles Banks. Stoddart and Yonge (1971) and Stoddart (1973) comprehensively summarized the geomorphology and ecology of Indian Ocean reefs. Montaggioni (2005) recently compiled and analyzed the available data on postglacial reef growth in the Indian and



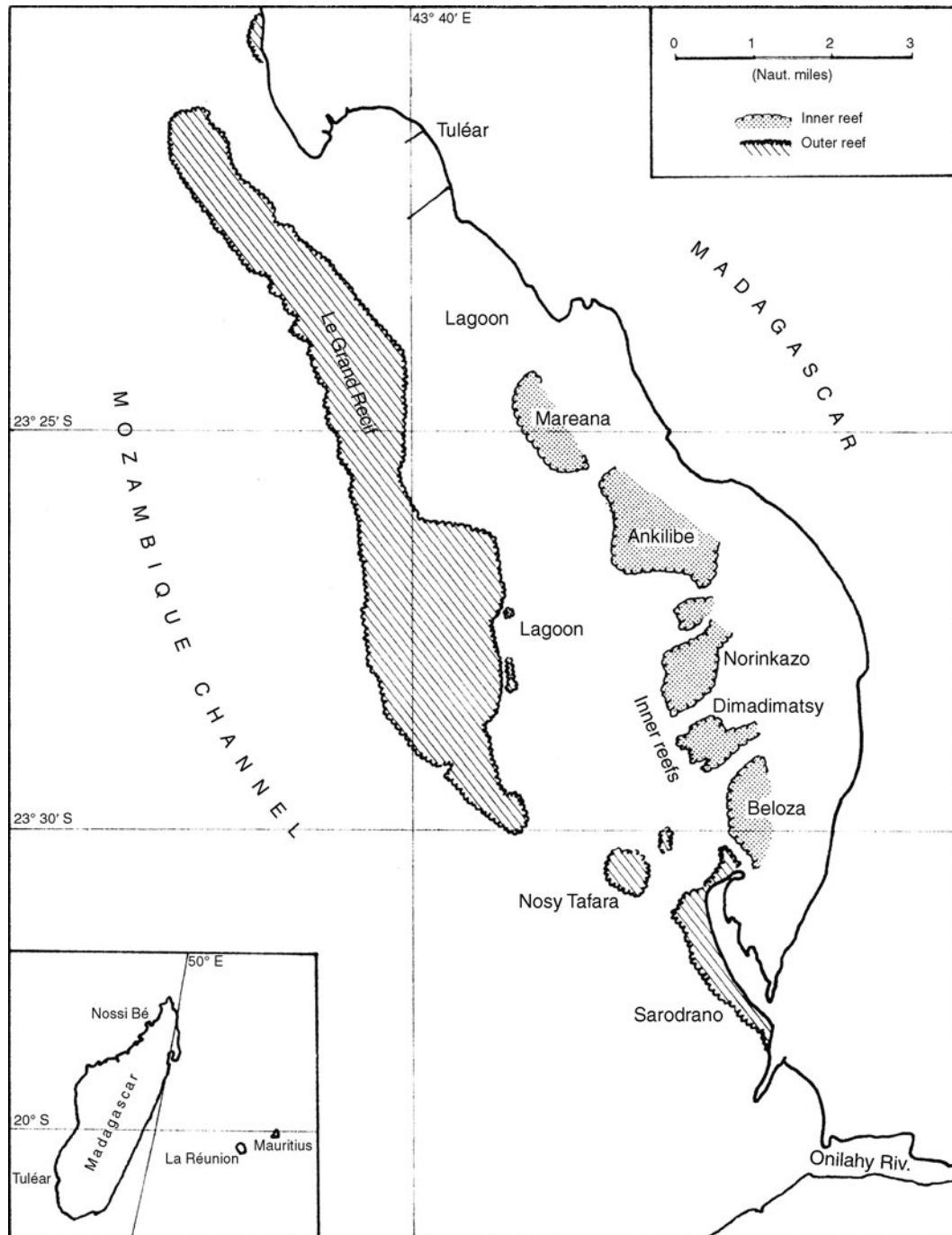
**Indian Ocean Reefs, Figure 1** Overview map showing major reef locations in the Indian Ocean (from Gischler et al., 2008).

Pacific Oceans. Here, an overview is given of well-studied locations of Madagascar, Mayotte, and the Maldives.

### Madagascar

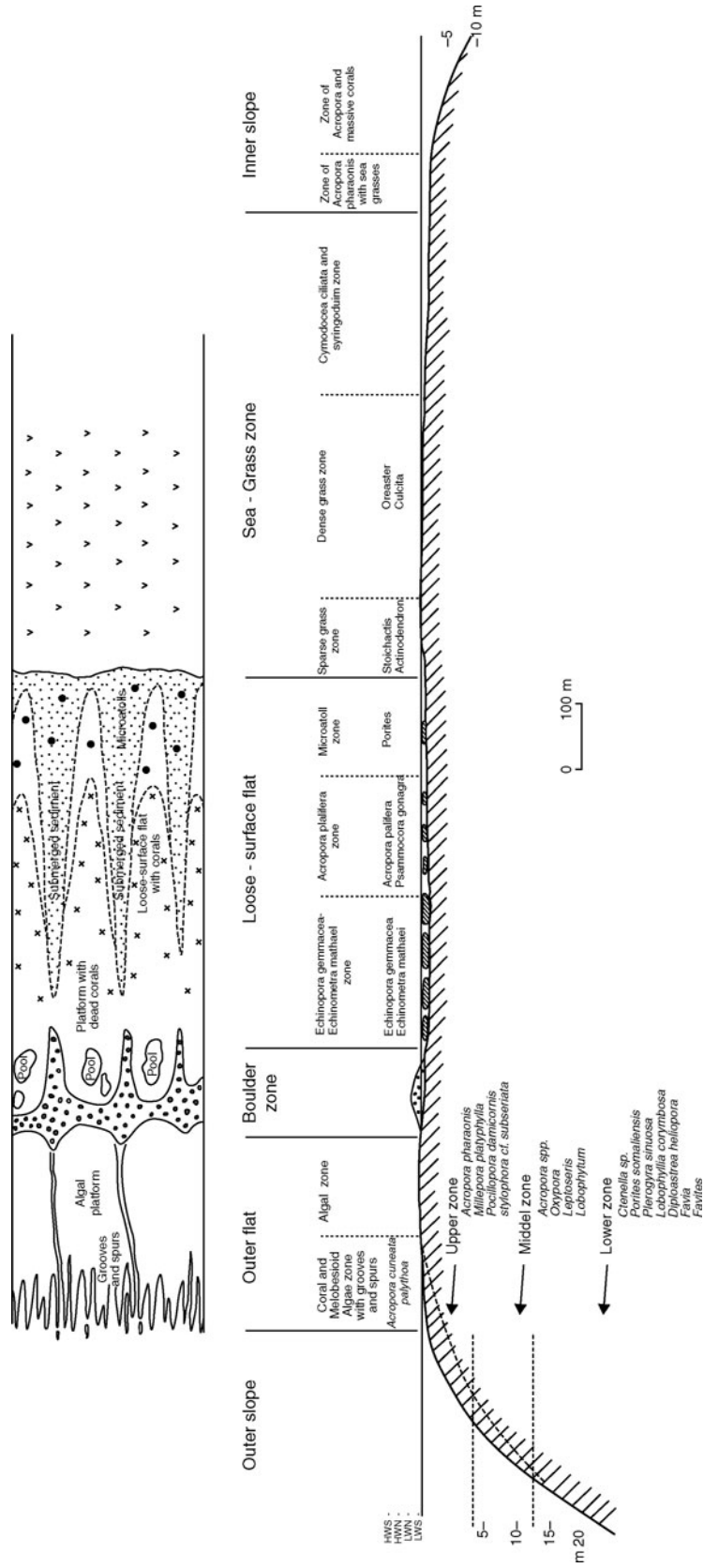
Numerous coral reefs are developed along the 4,000 km long coastline of Madagascar. They are much more common on the western than the eastern side. The climate is

tropical-subtropical. Strong SW winds predominate throughout the year, and cyclones reach the island frequently. There are numerous fringing reefs along the western Madagascar coast, but the best studied reef system is the offshore Grand Récif near Toliara (formerly Tuléar), at the southwestern coast of Madagascar (Figure 2). Grand Récif, is about 1.5 km across and 25 km long, and the

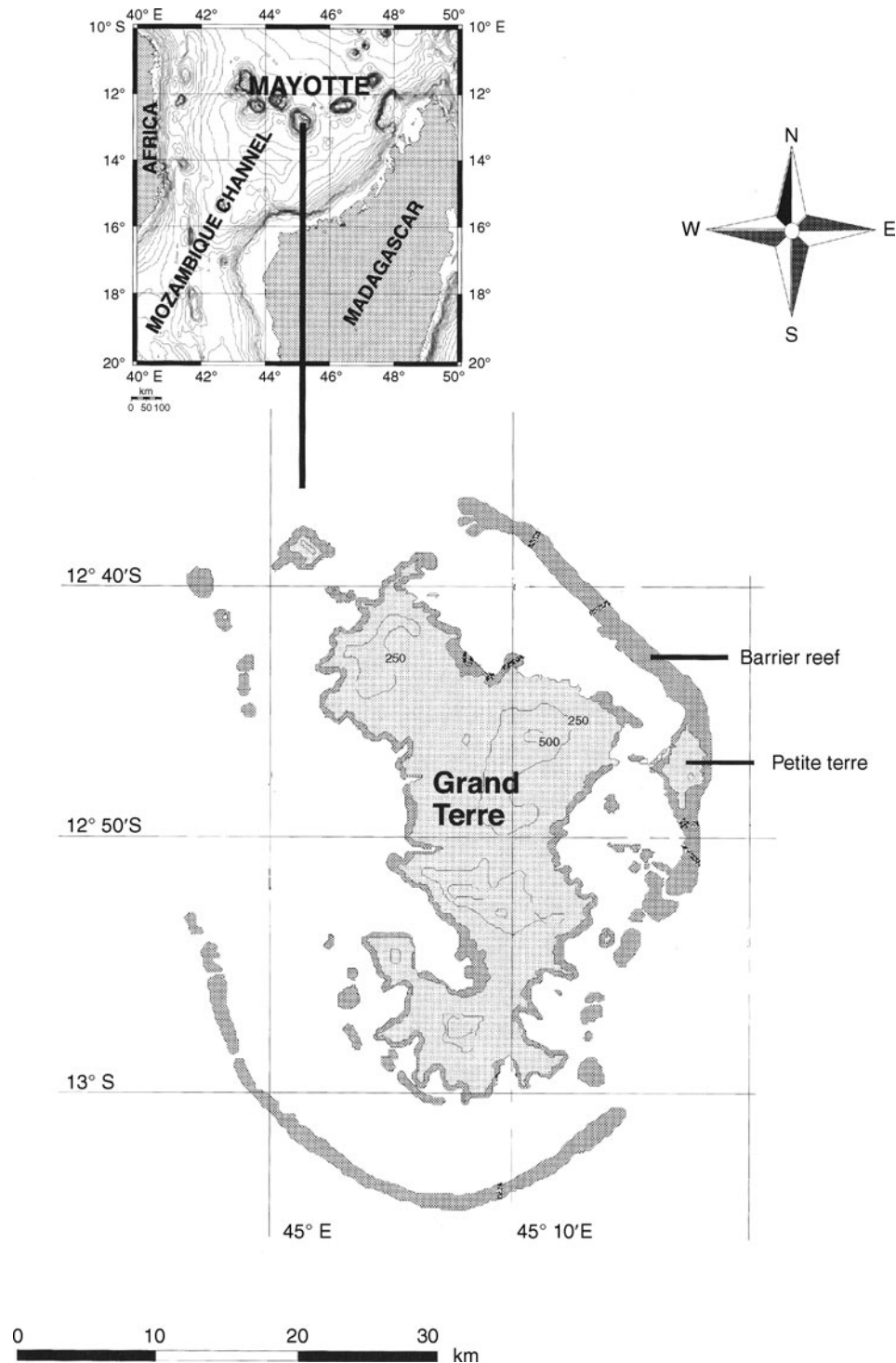


Indian Ocean Reefs, Figure 2 Map and location of Grand Recif, Madagascar (from Pichon, 1971).





Indian Ocean Reefs, Figure 3 Zones of Grand Recif of Toliara, Madagascar (after Pichon, 1964).



Indian Ocean Reefs, Figure 4 Map of Mayotte (from Zinke et al., 2001).

distance from its outer margin to the shore increases from 2 km in the north to 9 km in the south. The lagoon has an average depth of 10 m, and is connected to the open ocean in the north and south by channels 15 and 20 m deep

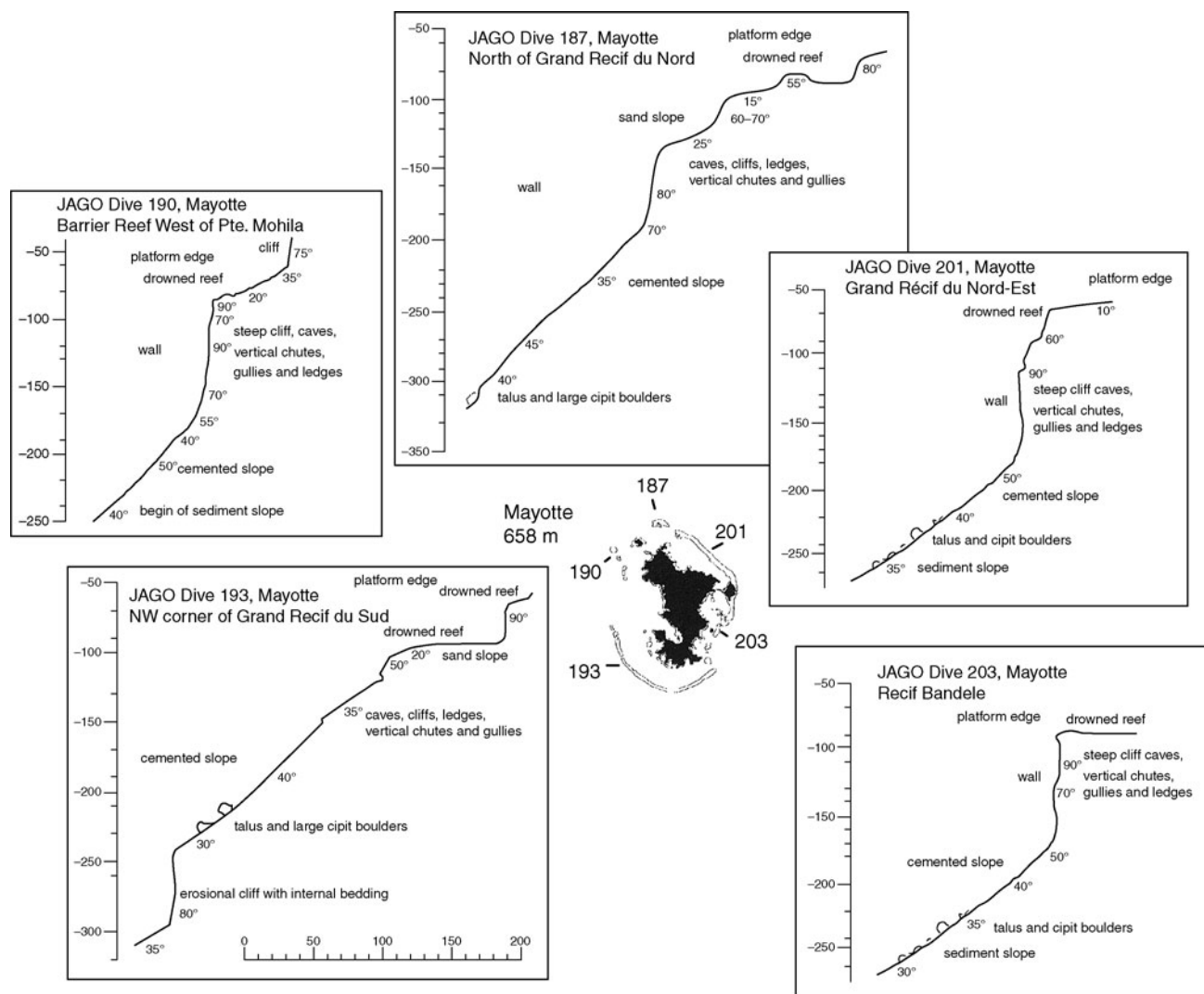
respectively (Pichon, 1971). Towards the south, small fringing reefs occur between the mainland and Grand Récif. Pichon (1964, 1978) distinguished seven reef zones across Grand Récif, which are from west to east (1) outer

slope spurs and grooves, (2) outer flat with spurs and grooves, (3) boulder zone, (4) loose-surface flat, (5) sea-grass, and (6) inner slope zones (Figure 3). More than 200 species of Scleractinian corals have been described from Grand Récif. Some authors refer to Grand Récif as a fringing reef (Pichon, 1964, 1971) and others as a barrier reef (Guilcher, 1988, p. 107). Similar problems of terminology exist for Ningaloo Reef on the western Australian coast. Both have sections that are “typical” narrow fringing reefs close to the shore, as well as offshore sections that are much larger, more complex, and separated from the shore by navigable channels up to several kilometers in width.

### Mayotte

The volcanic island of Mayotte in the western Indian Ocean covers an area of 375 km<sup>2</sup> and is 660 m high

(Figure 4). There is a surrounding barrier reef that is up to 2 km wide and interrupted by deep (60–80 m) channels. Four small sand cays occur on the barrier reef. In the NW, the barrier reef has a wide gap. Interestingly, some areas of the barrier reef form ribbons and faroes comparable to marginal reefs in the Maldives (see below). The lagoon inside the barrier reef covers some 1,500 km<sup>2</sup>, is up to 15 km wide, and reaches a depth of 80 m (Guilcher, 1971). Coral pinnacle reefs occur within the lagoon; fringing reefs are found at the Mayotte island shore. Dullo et al. (1998) investigated the forereef area in a submersible, and found a spur and groove system with mainly acroporid corals to 20 m depth. Below, a cliff and talus slope occurs. A drowned reef terrace occurs at about 90–100 m depth. From 90 to 190 m depth, a vertical wall transitions into another loose sediment slope extending beyond 300 m of water (Figure 5). Masse et al. (1989) recognized five



Indian Ocean Reefs, Figure 5 Mayotte forereef morphology (from Dullo et al., 1998).



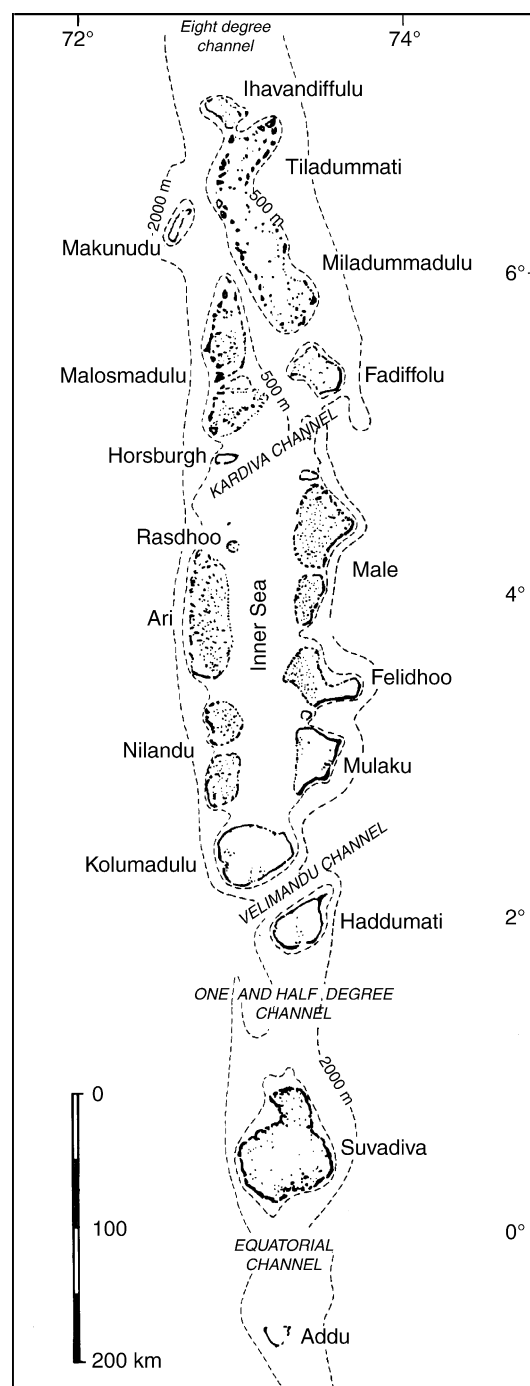
sedimentary facies including (1) coral-mollusk facies of the outer barrier reef, (2) coral-red algal facies of the reef flat, (3) mollusk-coral and (4) mollusk-*Halimeda* facies of the lagoon, and (5) mollusk-foram facies of the deep lagoonal plains. Guilcher (1971) compared the Mayotte barrier reef with south Pacific (Polynesian) barrier reefs and noted that a major difference is the lack of a distinct algal ridge and larger cays (motu).

## Maldives

The Maldives archipelago is about 1,000 km long and 200 km wide. There are 20 major atolls (Naseer and Hatcher, 2004), which are among the largest in the world (Figure 6). The climate situation is controlled by the Indian monsoon system with the windy and wet months of May–October and the dry and calm months of November–April. Due to their proximity to the equator, the Maldives are largely free of cyclones. From north to south, marginal reefs get more and more continuous. A total of about 1,500 small islands are located on marginal and lagoonal reefs. Atoll lagoon depths increase from about 50 to 60 m in the north to >80 m in the south (Woodroffe, 2005). Precipitation rates increase in the same direction from 1,650 to 2,400 mm/year. Marginal reefs have ribbon shapes and are in many cases developed as faroes. Faroes also occur within atoll lagoons. Their development has been explained by karst dissolution during Pleistocene sea-level lowstands (Purdy and Bertram, 1993). Reef zonation (Figure 7) based on coral occurrences has been elaborated by Stoddart (1966) and Ciarapica and Passeri (1993). In 1998, the Maldives reefs were heavily affected by the worldwide coral bleaching event (Schuhmacher et al., 2005). Modern sediment distribution is characterized by five facies (Gischler, 2006). Coral grainstone with coralline algae, *Halimeda*, and mollusks occurs on marginal and lagoonal reefs and islands. Skeletal grains in atoll-interior lagoons are mainly mollusks and foraminifera. There are true mudstones, mollusk wackestones, and mollusk-foram packstones, as well as hardgrounds that extend from channels through the atoll reef margins into the adjacent lagoon area.

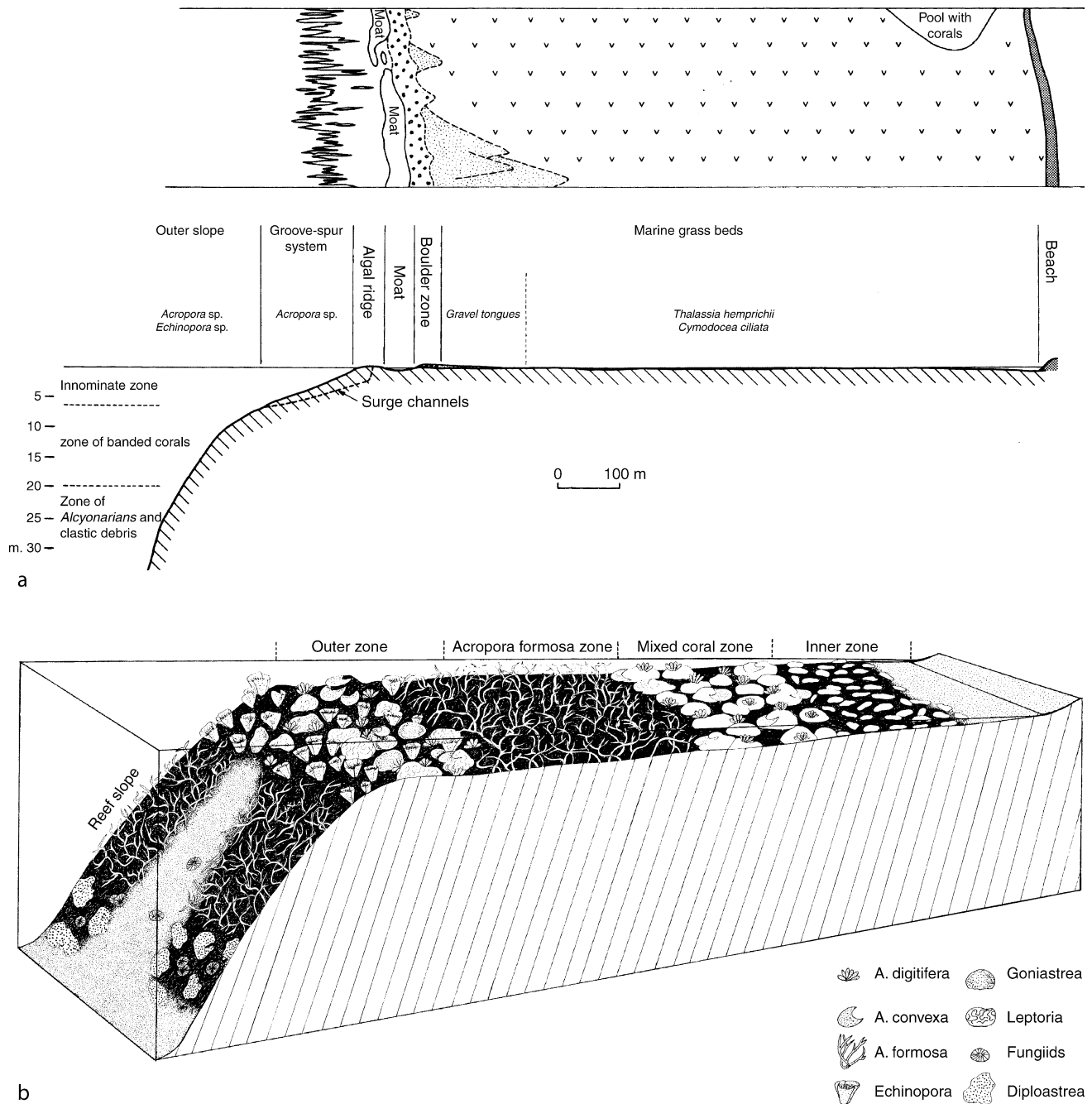
## Postglacial development

The Holocene fringing reef of Grand Recif (Toliara) is about 15 m thick. Reef growth started 6.6–8.3 kyrs BP and is predominated by robust branching coral, sands, and rubble (Camoin et al., 2004; Montaggioni, 2005). Reef accretion is characterized by a “catch-up” anatomy (see *Holocene Reefs: Thickness and Characteristics*). A drill core on the eastern margin of the Mayotte barrier reef recovered branched *Acropora* to a depth of 21 m and massive *Porites* to 30 m (Camoin et al., 2004). Reef growth started around 9.6 kyrs BP and is characterized by a keep-up anatomy. Zinke et al. (2001, 2005) investigated the lagoonal history of the Mayotte barrier reef lagoon using coring and shallow seismics. They found several sedimentary and seismic sequences including



Indian Ocean Reefs, Figure 6 Map of Maldivian archipelago (from Gischler et al., 2008).

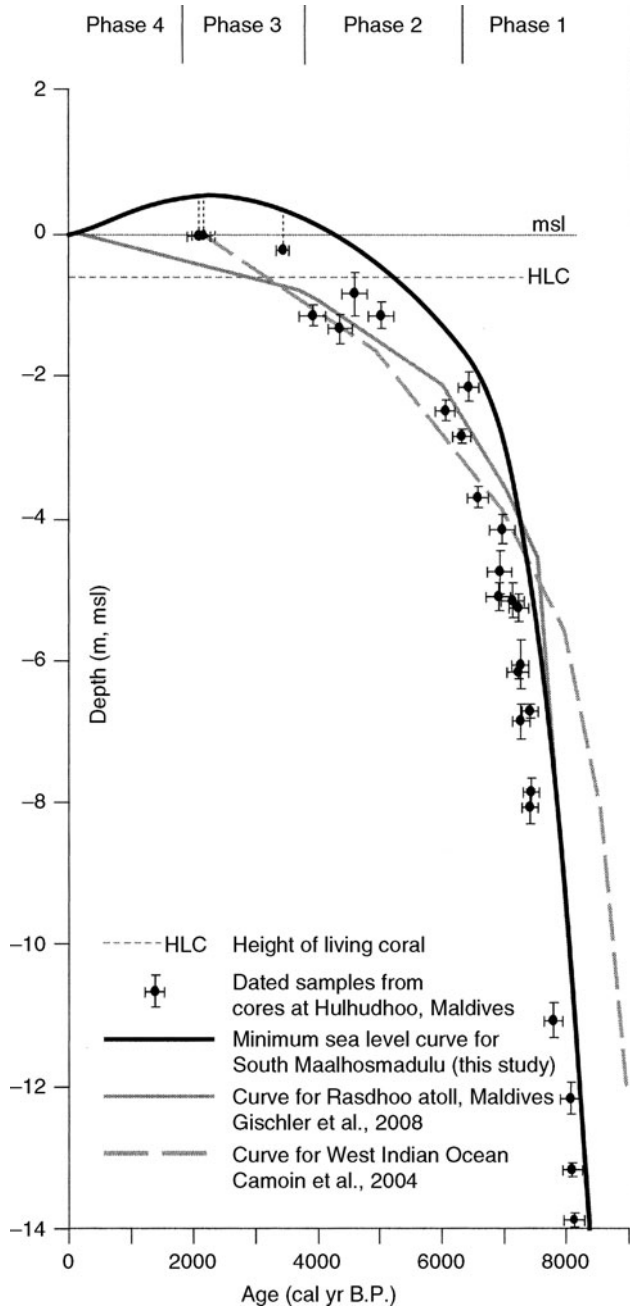
lowstand, transgressive, and highstand systems tracts. The thickness of the sediment fill is up to 20 m, but ample accommodation space remains. Two systematic studies on Holocene reef growth have been performed in the Maldives. Gischler et al. (2008) found Holocene reefs >20 m thick dominated by robust branching acroporids



**Indian Ocean Reefs, Figure 7** Reef zonation in the Maldives. (a) Marginal reef (from Stoddart, 1973). (b) Lagoonal reef (from Spencer Davies et al., 1971).

in marginal sites and massive corals (*Porites*) and sand and rubble facies in lagoonal reef sites. Reef growth started no later than 8.5 kyrs BP. Marginal reefs belong to the keep-up and lagoonal reefs to the catch-up types. Late Pleistocene reef limestone from marine isotope stage 5e (135 kyears BP) underlies the Holocene reefs. Kench et al. (2009) found comparable reef thicknesses and timings of reef growth; however, their cores were dominated

by massive corals, possibly due to the more protected drill sites as compared to the ones of Gischler et al. (2008). In addition, Kench et al. (2009) concluded that late Holocene sea level exceeded the modern one by 0.5 m from 4 kyrs BP, based on microatoll data (Figure 8). Holocene sea level in the Indian Ocean in general is controversial, in that both transgressive and transgressive-regressive curves have been proposed (Camoin et al., 2004; Woodroffe,



**Indian Ocean Reefs, Figure 8** Holocene sea-level curves for western Indian Ocean (from Kench et al., 2009).

2005; Gischler et al., 2008; Kench et al., 2009). More data, especially from the late Holocene, is needed.

## Summary

Indian Ocean reefs include numerous fringing reefs and atolls but only one true barrier reef. Reefs of Toliara (Madagascar), Mayotte, and the Maldivian archipelago are described. These reefs all show zonation and all are

dominated by corals. Massive and branched forms make up the postglacial reefs, which reach thicknesses of up to 30 m with high accretion rates of  $>10$  m/kyr. Modern sediment facies are characterized by skeletal grains. Holocene sea levels obtained from reef studies are controversial, and transgressive and transgressive-regressive curves are discussed.

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## Cross-references

Cocos (Keeling) Islands  
 Eastern Caribbean Coral Reefs  
 Holocene Reefs: Thickness and Characteristics  
 Maldives  
 Pacific Coral Reefs: An Introduction  
 Tsunami  
 Western Atlantic/Caribbean, Coral Reefs  
 Western Indian Ocean

## INDONESIAN REEFS

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### Definition

The Republic of Indonesia comprises >17,500 islands, straddling the equator in Southeast Asia. Its total land area is around 2 million km<sup>2</sup>, its territorial seas cover about 3.6 million km<sup>2</sup>, its living coral reefs are estimated to cover ~50,000 km<sup>2</sup>, and fossil reefs are commonplace across the archipelago.

### Introduction

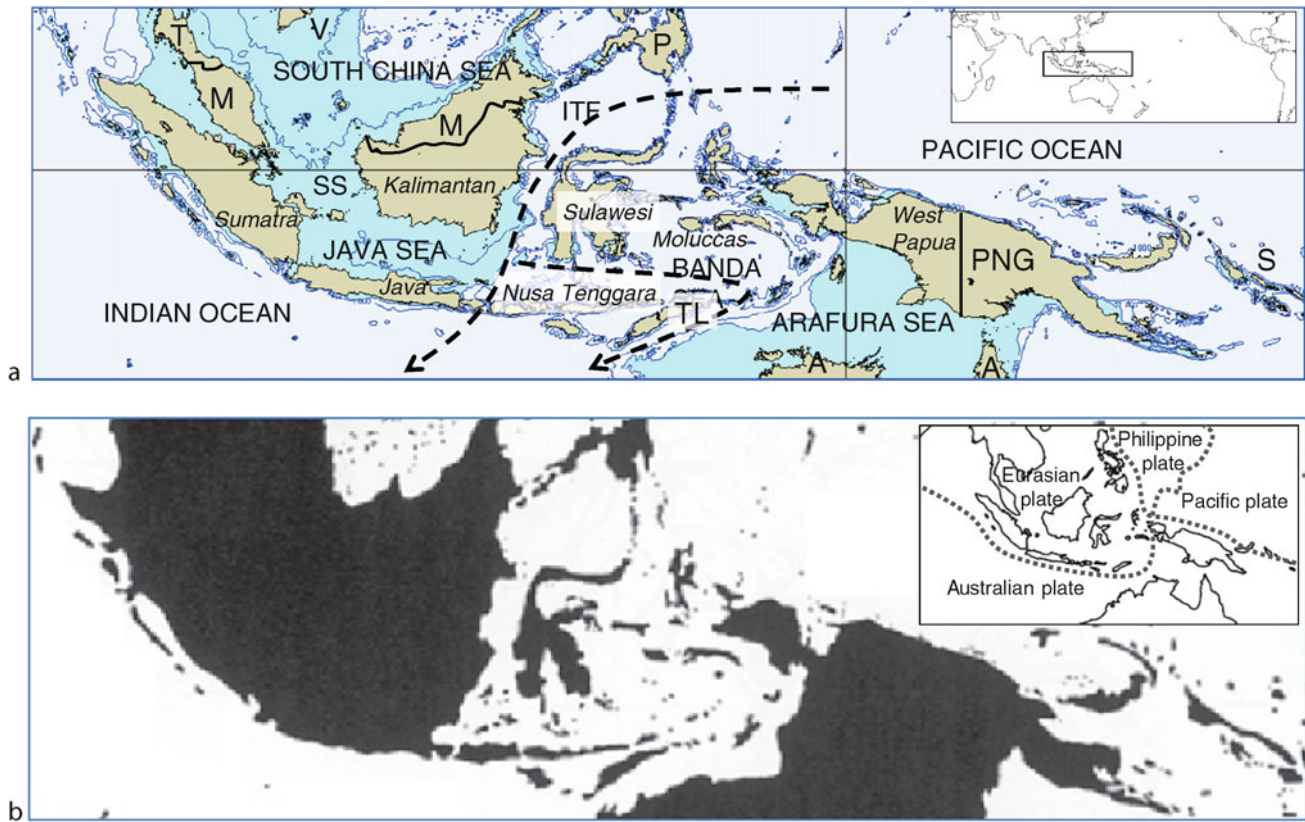
Indonesia is a vast nation with more enclosed seas than any other on earth. Straddling the equator (from 6°N to 11°S) over a north–south distance of 2,210 km (Figure 1a), about the same as the length of the Great Barrier Reef and three times the length of the UK), the country extends 5,271 km from east to west (almost 1 ½ times the distance from New York to Los Angeles). Indonesia's total land-sea area is ~4,573,400 km<sup>2</sup>,

comprising 42% land and 58% sea. The coastline – against which many coral reefs lie – is 95,000 km long (Tomascik et al., 1997), about 45 times longer than Australia's Great Barrier Reef. Total coral reef area has been estimated at 51,000 km<sup>2</sup> (about twice that of the Great Barrier Reef), excluding subsurface reefs and those in remote areas that have not been mapped (Burke et al., 2002). Indonesian seas include 960,000 km<sup>2</sup> of shelf seas <200 m deep (mainly in the west) and 1,694,000 km<sup>2</sup> of deep seas (Dahuri et al., 2009), mainly in the east, but also to the west and south of the narrow shelves bordering the island arc from Sumatra to Nusa Tenggara (Figure 1a). Together, these deep and shallow seas afford a wide range of environments for reef development and populations of coral reef species, from shallow sheltered bays to deep swell-exposed outer slopes (see entry *Coral: Environmental Controls on Growth*). There are also large sections of Indonesia's coasts and seas from which coral reefs are absent. These are of two general types. The first are those sheltered shallow areas facing the inner shelf that are too muddy for corals and thus for the development of coral reefs. The second are a number of long sections of Indian-Ocean-facing coasts, along which corals can be found, but from which major reef development is excluded, probably by extreme wave forces (Spalding et al., 2001). In addition to the present environmental diversity, the effects of eustatic sea-level changes and high tectonism contribute to the diversity of form and biotic composition of Indonesia's coral reefs (Hutomo and Moosa, 2005). Four major tectonic plates meet in Indonesian seas (Australian, Eurasian, Philippines, and the Pacific; Figure 1b), and the consequent high levels of volcanism and seismicity have great significance for the size, development, and morphology of Indonesia's coral reefs, both fossil and modern.

The main focus of this entry is physical geography – the extent, distribution, and types of coral reefs, and the variability of their environmental settings and historical drivers. In Indonesia, people are important drivers of living reef condition and productivity: much of Indonesia's population of more than 250 million people lives close to reefs, harvests reef resources (food, building materials (Figure 3)), and modifies reef habitat and water quality through dredging and land-use in adjacent catchments. The people–reef interaction is the focus of much research, management, and conservation attention (Nontji, 2002; Anon, 2009).

### Biodiversity

Indonesia is at the center of the “Coral Triangle” containing Earth's greatest biodiversity of marine life (e.g., 76% of all corals; 37% of all coral reef fishes and similar proportions of other marine life, Hoeksema, 2007; Hoegh-Guldberg et al., 2009). The greatest diversity of corals and fishes occurs in the deeper seas of Eastern Indonesia on the Pacific Plate (“Wallacea”) (see entry *East Indies Triangle of Biodiversity*), which is where the most Indo-West Pacific species show overlaps in their



**Indonesian Reefs, Figure 1** Indonesia and neighboring countries. (a) Main regions and bathymetry (with depths <200 m in darker blue) and location (inset). Abbreviations: A Australia; ITF Indonesia Throughflow (dashed lines); M Malaysia; P Philippines; PNG Papua New Guinea; S Solomon Islands; SS Sunda Shelf; T Thailand; TL Timor-Leste; V Vietnam. (b) Geography at time of last glacial maximum 17–18 kya when sea level was ~120 m lower than the present. (Source: Hoeksema, 2007. Inset: Four tectonic plates that converge in Indonesia).

distribution ranges. Some larval dispersing crustacea (Barber et al., 2000) and coral species (Hoeksema, 2007) that are abundant in Wallacea do not occur on Sunda Shelf reefs in the west, suggesting there have been limits to their dispersal and/or population establishment in the transgression following the LGM (17–18 kya). However, while there are some coral species that do have distributions that overlap only with the Indian Ocean or only with the Pacific Ocean (Wallace and Wolstenholme, 1998), there are many other coral species that do occur across the archipelago (Edinger et al., 2000; Wallace and Wolstenholme, 1998).

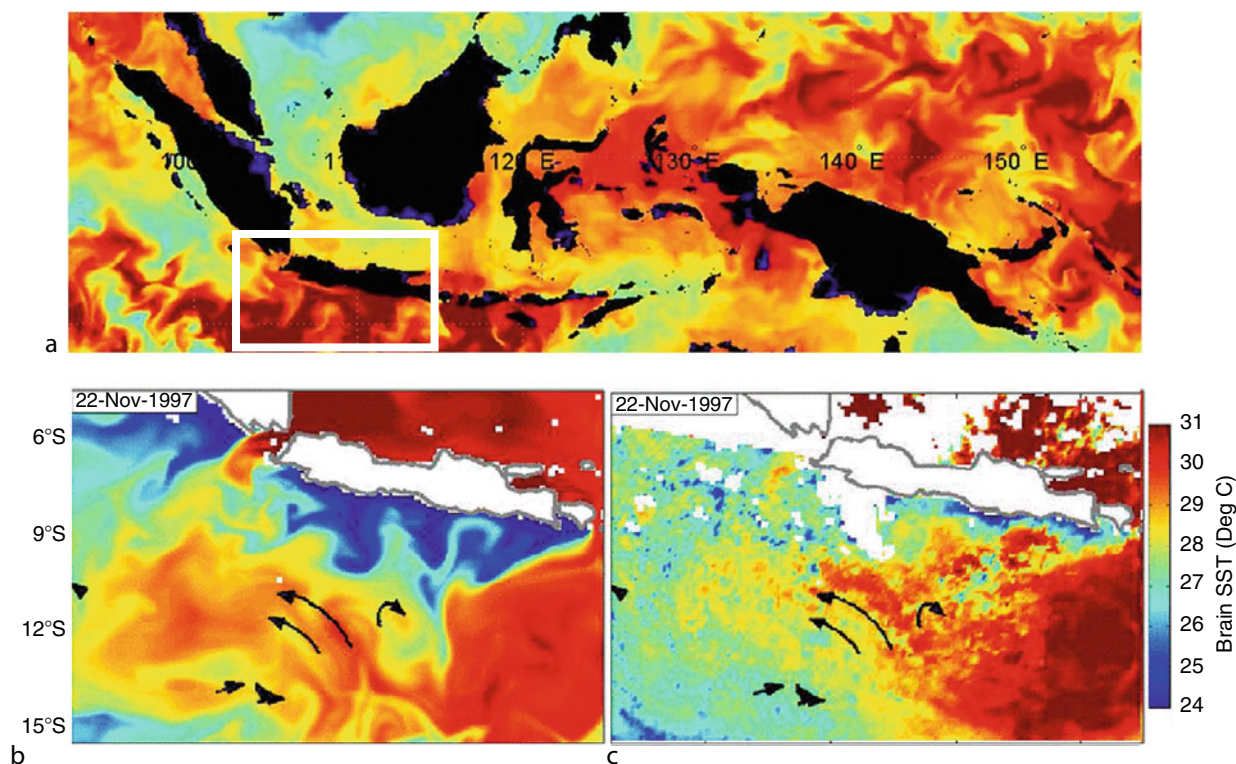
Whereas the origins of this diversity is explained in large part in terms of sea-level and oceanographic changes and isolation leading to speciation in geological and evolutionary time (Barber et al., 2000; see entry *East Indies Triangle of Biodiversity*), a great deal of the diversity and productivity of marine life in Indonesia today (Tomascik et al., 1997; Hoeksema, 2007) is maintained by the immense extent and variety of its coral reefs. Despite the drying of Indonesia's continental shelves during Pleistocene lowstands (Figure 1b), the dominant corals on modern reefs on the shallow Sunda Shelf in the

west are largely similar to those of the open ocean reefs of eastern Indonesia (Edinger et al., 2000). The seafloor topographic highs and submarine slopes of the latter area apparently afforded sufficient extent and temporal continuity of suitable habitat for reef biota to survive the lowstands. Moreover, there has clearly been adequate time since the last glacial maximum for all the vital functional groups of reef biota (Done et al., 1996) to disperse to and develop reefs in the newly submerging shelves 20–7 kya, albeit with the local variability in species composition referred to above (Barber et al., 2000; Hoeksema, 2007).

### Environmental setting

Indonesia's vast extent and physical complexity provide a range of environmental settings for coral reefs almost as wide as that of the entire global coral reef domain. Ocean waves and swells with long fetches across the Indian Ocean break on reefs around islands along the west coast of Sumatra and on headlands and semi-enclosed bays on the south coast of Java. Cool nutrient-rich waters regularly upwell onto western and southern margins of





**Indonesian Reefs, Figure 2** Modeled and satellite remote sensed sea surface temperatures (SST) and modelled currents. (a) March 27, 2004 (no upwelling). Produced by: C. Steinberg, Australian Institute of Marine Science, using Bran1 database <http://www.marine.csiro.au/blueink/> (b) Bran1 representation of SST on Nov 22, 1997 during a period of strong upwelling. (c) AVHRR SST. Source of (b) and (c): Oke et al., 2005.

Sumatra, Java, and Nusa Tenggara, while waters only a few kilometers away can be near 30°C on the same day (Figure 2). Reefs in the Indonesian Throughflow (ITF; Figure 1a) are regularly exposed to southward surface currents of  $\sim 0.8 \text{ m s}^{-1}$  (week-long average; Gordon et al., 2003), whereas many reefs in deep embayments, away from the ITF are subject only to weak tidal flows. Reefs throughout most of the country are periodically exposed to currents and waves generated by monsoonal winds. Only a small proportion of Indonesia is in the cyclone belt ( $>7^\circ\text{S}$ ), so only the southernmost reefs are exposed to the extreme physical destruction wrought by cyclones (see entry *Tropical Cyclone/Hurricane*). An example is Nusa Tenggara (Figure 1a), which is a region of cyclone genesis for cyclones that move onto Australia's north-west coast, and where destructive seas are important drivers of coral mortality and reef growth (Tomascik et al., 1997). Massive waves (see entry *Tsunami*) and seismic displacement (up or down) are also commonplace (Richmond et al., 2006; Briggs et al., 2006) (see entry *Earthquakes and Emergence or Submergence of Coral Reefs*). For example, the earthquake of December 26, 2004 (9.3 on the Richter scale) caused the death of 300,000 people across the Indian Ocean. The epicenter was just off the west coast of Sumatra and initial reports

from satellite observations suggested 97,250 km of reef was affected in Indonesia with a loss of 3,061 ha valued at \$332 million (Campbell et al., 2007). However, more detailed survey subsequently indicated that the near-field damage was much less than originally estimated. Both uplift and subsidence were recorded but Hagan et al. (2007) suggested that much of the damage was caused by terrestrial debris washed onto the reef, and that the reefs were already in poor condition due to anthropogenic causes (Hagan et al., 2007), "...the initial damage to corals, while occasionally spectacular, was surprisingly limited and trivial when compared to pre-existing damage most probably caused by destructive fishing practices" (Campbell et al., 2007, p. 55).

### Fossil reefs

Fossil reefs abound in Indonesia, reflecting both tectonic uplift and eustatic sea-level changes. On Atauro (Chappell and Veeh, 1978), Alor (Hantoro et al., 1994), and Sumba Islands (Verstappen, 1997), for example, there are Pleistocene coral reef terraces up to 475 m above sea level. The highest and oldest of these terraces formed 1000 kya suggesting average uplift rates of,  $0.49\text{--}1.0 \text{ mm y}^{-1}$ . The lower terraces correspond with high sea levels of specific interglacial stages at 275–117 kya, 344–228 kya,





**Indonesian Reefs, Figure 3** (a) Fringing reef adjacent to a village in the district of Kendari, Southeast Sulawesi, 2003. Composite image from a single digital photo by Yul. (b) Land reclamation using live and dead coral, Kepulauan Seribu, Java, 2005. Photo: T. Done. (c) *Porites* coral head in village square, Pulau Hinako, Sumatra, 2005. Photo: T. Done. (d) Raised reef flat following December 2004 earthquake, Lahewa Village, Nias, Sumatra. February, 2005. Photo: Nurul Dewani.

397–322 kya, and 603–584 kya (Pirazzoli et al., 1991). There is also widespread occurrence of younger fossil reefs to ~5 m above current sea level representing upward limits of reef growth determined by Holocene sea-levels.

The 5 m reef is believed to have been formed at a high stand about 5.8 kya, and there are fossil coral heads (Figure 3c) and reefs interpreted as representing progressively lower sea-level highs at 4 kya, 2.6–2.9 kya,

and 0.2 kya (Tjia, 1996). Finally, there are geologic features caused by events within recent human memory. For example, the major earthquake of March 2005 lifted reefs off the east coast of the island of Nias by  $>2$  m, and sunk those on its west coast by  $\sim 0.25$  m (Briggs et al., 2006).

### Living reefs

Indonesia's coral reefs include all the major morphological forms: viz. atolls, barrier reefs, patch reefs, and fringing reefs (Tomascik et al., 1997). There are also coral communities (no tendency for reef development) and incipient reefs (which do accrete framework, but have not yet built substantive framework; see entry *Coral Reef, Definition*) on most coastal hard substrata (fluvial bars; rocky shores). Coral communities and incipient reefs occur on stable shores of active volcanoes (Tomascik et al., 1996; Starger et al., 2010), while true fringing reefs and barrier reefs occur only on non-volcanic islands and older quiescent volcanoes. Indonesia's "atolls" (annular forms with enclosed lagoon) occur in the currently tectonically active Banda Sea (Figure 1a), but many are probably sitting on non-volcanic basements. There is a preponderance of uplifted reefs in the area that suggests that over geological time scales, Indonesia's atoll basements are frequently subject to diastrophic deformation (Tomascik et al., 1997). Indonesian atolls may be examples of those for which Purdy and Winterer (2000) invoke dissolution caused by annual monsoon rains as major drivers of lagoon depths. The process is highly plausible for atolls in Indonesia, whose antecedent foundations would have been exposed during LGM to annual rainfall presumably measured in meters (assuming, after Purdy and Winterer (2000) that today's rainfall is a good proxy for LGM rainfall). In this regard, Indonesia's atolls contrast both with Darwin's classic genetic sequence of atoll formation (which does not rely on massive dissolution), and with Grigg's (1982) Darwin Point elaboration, (which involves plate movement into less hospitable waters (see entries *Darwin, Charles (1809–1882); Darwin Point; Subsidence Hypotheses of Reef Development and Volcanic Loading and Isostasy*)). In Indonesia, reef development also occurs in turbid waters along some open sedimentary coastlines, within muddy coastal embayments, and around high continental islands. In these situations, frequently in shallow-water (5–20 m) depths, reef growth can be very rapid, with reefs reaching sea level and undergoing significant seaward progradation over century to millennial time scales (see entry *Turbid Zone and Terrigenous Sediment Influenced Reefs*).

### Sumatra

The wave-exposed west-facing coasts of Sumatra facing the Indian Ocean (Figure 1a) are characterized by steep headlands and intervening beach-ridge coastal plains and deeply incised river valleys (Richmond et al., 2006). There are patchy fringing coral reefs in coastal bays and nearshore continental islands, but much stronger reef

growth occurs on the continental islands that extend in a line from Simeulue, through Nias, Banyak, Batu, and Mentawai Islands. These islands are separated from Sumatra by marine basins 1–2 km deep, and all have substantial fringing coral reefs. On open west-facing coasts, these reefs are usually patchy and narrow, but semi-enclosed bays on all sides, and on points that deflect ocean waves, they are up to several hundred meters wide. A few kilometers to the west of Nias on the 200 m isobath are the inhabited Hinako Islands (low, vegetated raised coral reefs with wide reefs; Figure 3c). At Sumatra's northern tip, modest fringing reefs are developed on continental islands of Pulau Aceh and Pulau Weh. However, reefs are absent from the entire 1,700 km of Sumatra's north and north-east facing coasts, which are mainly muddy prograding shores with mangrove forests. There are well-developed fringing reefs in the islands of the Riau Archipelago and Natuna Sea, between Sumatra and Kalimantan.

### Java

Java's reefs primarily comprise coral cays and island fringing reefs offshore from its muddy north coast. The 700 reefs of Kepulauan Seribu, 20–80 km offshore from Jakarta, are coral cays. These reefs are characterized by a gradient of increasing coral diversity and water clarity with increasing distance offshore (DeVantier et al., 1995). The Karimunjawa group (70 islands about 80 km offshore from central Java), are high islands with well-developed fringing reefs, barriers, and lagoons. There are reefs scattered along the 800 km south coast of Java, favoring points where waves approach at oblique angles. Limited reef-flat development elsewhere along this shore is probably a result of extremely strong waves (Spalding et al., 2001). However there are well-developed fringing reefs along Java's short and more sheltered east coast (Spalding et al., 2001).

### Kalimantan

The Mahakam River, which drains almost one third of East Kalimantan, is a major influence on reef distribution. On the east coast, there are only occasional fringing reefs and offshore patch reefs, for example, in front of Balikpapan Bay. Immediately to the north of the Mahakam Delta, there are well-developed fringing reefs, interrupted by other rivers, while northwards to the border with Sabah the coastline is reefless, dominated by major river deltas. The southwestern coast of South Kalimantan is also largely deltaic and devoid of reefs, but to the east and north of Tanjung Selatan there is some fringing-reef development. There are three barrier-reef systems east of Kalimantan: the submerged Great Sunda Barrier Reef (630 km) lies 60 km offshore along the 200 m isobath, and smaller barrier reefs are found north of the Mahakam delta. North of the Mangkalihat Peninsula and 60 km offshore are three major lagoonal shelf reefs: Muaras (288 km<sup>2</sup>), Maratua



(690 km<sup>2</sup>), and Kakaban (21 km<sup>2</sup>). The latter two have raised limestone rims up to 120 m above sea level.

### Sulawesi

The island of Sulawesi (coastline 4,750 km), probably has the largest coral-reef area in Indonesia. A very high proportion of its coastline and offshore islands is fringed with reefs often ~200 m wide. Tomascik et al. (1997) describe 34 individual barrier reefs around the islands with a total length of 2,084 km, that is, bordering 43% of Sulawesi's coastline, and of which eight are more than 100 km long. These very long barrier reefs are submerged over most of their lengths, but many shorter ones a few kilometers offshore of islands are classic intertidal reefs separated from the shore by navigable lagoons (see entry *Coral Reef, Definition*). The Spermonde Archipelago comprises some small-platform reefs with cays, many submerged platform reefs, and a fragmented submerged barrier reef that lies 45–65 km offshore. There are also long submerged barrier reefs running eastwards from the volcanic Togian Islands (165 km) and along the southern margins of the Banggai Islands (175 km), including faro reefs similar to those found in the Maldives. Tomascik et al. (1997) describe 27 "atolls" in the waters around Sulawesi, though it is doubtful whether many have developed from volcanic foundations. There are numerous submerged reefs and a further 27 "oceanic" or "platform" reefs at the sea surface, including open-water reefs associated with continental (not always volcanic) islands. They occur in clusters around to the southwest and west of Makassar, the south of Teluk Bone (including World Heritage-nominated Taka Bone Rate), and the southeast, where there is a group of reef-fringed high islands known collectively as Wakatobi (Pulau Wangiwangi; P. Kaledupa; P. Tomea; P. Binongko).

### Bali and Nusa Tenggara

These islands are all part of one of the world's most active volcanic island arcs, formed at a tectonic plate subduction zone. Fringing reefs are ubiquitous, their morphologies depending on the geomorphology of the coastline and the tectonic history of the islands. Many are narrow structures 30–100 m wide with an intertidal reef flat and very sharp seaward drop-off. However, much wider reefs are also present. For example, around Bali, van Woesik (1997) indicates the fringing reefs extend 500 m from the shoreline. There are also well-developed reefs at Komodo National Park (Djohani et al., 1999) and Lembata Island, with three active volcanoes (Tomascik et al., 1997). Discontinuous fringing reefs with well-developed spur and groove systems occur along the high energy southern shore of the Nusa Tenggara islands. On the more sheltered western and north-western sides facing the Flores Sea, the reefs are more continuous and up to 800 m wide, with dense growth of sea grasses on the flats. Some nine barrier reefs are listed by Tomascik et al. (1997) in this region, though some are very close to shore and difficult to differentiate from fringing reefs with "boat

channels." At least a third of the north coast of Flores is bordered by such a barrier with other significant barriers on both north and south coasts of Sumbawa and the north coast of Lombok. No open water reefs are found to the south of the island arc, probably because of the great depth of water. There are only two in the Flores/Banda Sea area off the northern shores of Flores (Karang Serbete and Gosong Boni).

### Maluku

The coral reefs of Maluku are regarded as the biologically richest in the world (Hoeksema, 2007). Fringing reefs thrive in the turbid waters of the Aru Islands, which consist of six main islands and 79 smaller islands separated by long narrow channels. Major fringing-reef development is along the shallow east coast where the reef can be up to 1.5 km wide, but narrower reefs are found along the remaining coastlines, except the southern part of the west coast. There are 15 reported barrier reefs with a total length of 425 km, but so little of this area has been surveyed in detail that this is probably an underestimate. They are associated with the islands of Morotai, Halmahera, Seram, Gorong, Kofiau, Obimayor, Batanme, Nila, and Tanimbar. Open water reefs, very few if any of which are true atolls, are found in the Banda Sea (Kepulauan Lucipara and Kep. Penyu), and to the south and east of Halmahera.

### West Papua

West Papua, with a coastline length of 4,200 km, remains one of the least studied areas in Indonesia. Because of high run-off and sediment yield, fringing reefs are missing from significant sections of the coastline, but in other places, fringing reefs appear to be very continuous. Tomascik et al. (1997) suggested the following as the major areas:

- The north coast from Jayapura to the border
- Jayapura to Tg. Kandara, where the reefs are 300–400 m wide and westwards to Sarmi
- All the islands of Cenderawasih Bay, 50–100 m wide
- On the south coast west of the Omba River
- The southern side of the "Bird's Neck" between Lakahia Bay and Kamarau Bay
- Between Tg. Tongerai and Tg. Kirana, the coastlines along the foothills of Kumafa and Fakfak Mountains, and
- The northern side of the "Bird's Head," which appears to be suitable for fringing reefs.

More recent studies have more than verified Tomascik et al.'s predictions. For example, more than 500 species of reef building corals have been reported at Raja Ampat (Turak and DeVantier, 2003), making it "the most diverse area of the Indo-Pacific" on record for corals.

### Summary

Indonesia's territorial seas are the world's largest contiguous coral reef domain under the sovereignty of a single



country. All major morphological forms of coral reef occur in Indonesian waters: atolls, barrier, fringing, platform, as well as coral communities (not building reefs), and incipient coral reefs. Many of the major barrier reefs are submerged structures that rise to depths of 15–10 m from near the 200 m isobath, reflecting their former existence as fringing reefs during periods of low sea level, brought to an end by the 120 m rise in sea level following the last glacial maximum, 18–17 kya. Most, if not all, “atolls” occur on sea-floor highs whose geology is not known, but is likely in most cases not to be volcanic. In Indonesia, atoll forms may, therefore, be better described as lagoonal platform reefs. Volcanic islands are extremely abundant, many with good reef development, but many also too active and/or too young to have permitted substantial reef development. There are abundant raised fossil reef terraces across the country, a result of upward displacement of islands by subduction beneath them of the Indian Ocean plate, by Pleistocene and Holocene sea-level fluctuations, and by seismic uplift. There are large and thriving modern reefs in both the deep eastern and shallow western parts of Indonesia’s enclosed seas, as well as along the south and westward shores facing the Indian Ocean. The biodiversity of Indonesia’s reefs – the highest of anywhere in the world – represents the overlap of four types of distributions: Indian Ocean, Pacific Ocean, Indian plus Pacific Ocean, and endemics (Wallace and Wolstenholme, 1998; Hoeksema, 2007). These overlaps are believed to be outcomes of geological history, sea-level fluctuations, and the barrier to west to east dispersal provided by the Indonesian Throughflow, which moves five times as much water from east to west than in the opposite direction (Gordon et al., 2003). Current reef diversity and productivity are sustained by an extremely complex physical and oceanographic setting.

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## Cross-references

[Coral Reef, Definition](#)  
[Corals: Environmental Controls on Growth](#)  
[Earthquakes and Emergence or Submergence of Coral Reefs](#)  
[East Indies Triangle of Biodiversity](#)  
[Plate Tectonics](#)  
[Tethys Ocean](#)  
[Tropical Cyclone/Hurricane](#)  
[Tsunami](#)  
[Volcanic Disturbances and Coral Reefs](#)

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## INFRASTRUCTURE AND REEF ISLANDS

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### Definitions

Infrastructure: Structures and facilities required to support human activities.

Reef Islands: (1) The portions of modern coral reefs permanently above high tide level – includes atoll islands (motus), coral cays, low wooded islands, mangrove islands. (2) Continental islands or raised ancient reefs completely or mostly surrounded by modern coral reefs or located within a coral reef region. These islands may have sedimentary margins which have formed or behave in similar ways to the various reef islands listed in definition (1).

### Introduction

Reef islands have been occupied by humans for many centuries, requiring the provision of various forms of infrastructure to support their communities. Groups of permanent settlements with similar cultural identity may form independent island nations, such as the Maldives in

the Indian Ocean ([Figure 1](#)), Kiribati, and other island nations in the Pacific and the Caribbean. Other regional groups of reef islands form parts of larger nations as in Indonesia, the Philippines or the Torres Strait Islands, the latter being politically part of Australia.

In other cases, human occupation was or is transient as infrastructure is set up to support some form of extractive industry such as guano mining for agricultural purposes, beche-de-mer fishing, or turtle canning. Tourism is a more recent and possibly less transient use of reef islands (Hopley et al., 2007).

Reefs and reef islands have been and continue to be used as platforms for structures and facilities needed as navigation aids and for communications and weather forecasting.

Reef islands (definition (1)) are inherently unstable and change their size, shape, elevation and location in response to short-term changes in wind, wave and current patterns and to long-term changes in sea levels. Their low elevation makes them particularly threatened by rising sea levels associated with climate change (see Chapters *Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity*; *Climate Change: Impact on Coral Reef Coasts*).

### Infrastructure for reef island communities

Inhabited reef islands require most types of basic infrastructure associated with coastal communities, including the provision of transport or access to the island, shelter in appropriate buildings, water supply, waste disposal (sewage and refuse disposal), electric power, communications, roads, and sea defence. Provision of much of this infrastructure involves changing the natural environment. Some activities, such as reclamations to enlarge islands for resort and other development that may be permitted in island nations, e.g., the Maldives (Bodge and Howard, 2007), are not allowed in conservation regions, e.g., Great Barrier Reef Marine Park.

Transport to and from an island requires:

- Appropriate mooring and/or harbor facilities for modern vessels, involving dredging of entrance channels and harbor basins through the reefs surrounding islands ([Figure 2](#)).
- Airfields and helipads constructed in lagoons or on reefs and islands ([Figure 3](#)).

Dredging harbor basins in reefs inevitably releases the silt and mud trapped in the cavities of the reef substrate ([Figure 4](#)) and, if this process is uncontrolled, significant damage may occur to the reef environment in the vicinity of the harbor works (Gourlay and Jell, 1993). Growth of corals may be inhibited by light reduction in turbid water or by smothering by deposited sediments. Artificial entrance channels to both dredged basins and atoll lagoons can concentrate and/or increase tidal flows on/off the reef or in/out of the lagoon with consequent long term changes to the reef or lagoon environment ([Figure 2](#)) (Maragos, 1993; Gourlay, 1995; Gourlay and Hacker, 2008). In some



**Infrastructure and Reef Islands, Figure 1** Male, capital city of the Maldives, occupies every square meter of its cay. Photo: [www.letsgomaldives.com](http://www.letsgomaldives.com). Reproduced with permission.



**Infrastructure and Reef Islands, Figure 2** Heron Island – southern Great Barrier Reef, Australia (GBR). Sand is being removed from reef top through channel dredged in reef rim. Photo: Peter Flood, January 1979.

places, e.g., the Maldives, sea planes provide a major form of interisland transport and their operation may require the removal of patch reefs and other obstructions from landing areas in lagoons.

Construction of airfields and roads on reef islands and surrounding reefs or in adjoining lagoons requires supplies of suitable filling material. In some cases, this will have to be coralline sand and gravel dredged from adjoining lagoons and in other cases terrigenous material quarried from an adjoining continental island. While coralline

sand and gravel filling material does not meet all the usually required technical specifications – it lacks fine sands – it can be used effectively for such reclamations (Bullen, 1991). All such dredging and reclamation projects pose the risk of undesirable environmental impacts.

Location of buildings on reef islands usually requires removal of vegetation and thereby interference with nesting sites for birds and turtles. Moreover, buildings need to be located away from the unstable portions of the island's shoreline. The most stable central portion of





**Infrastructure and Reef Islands, Figure 3** Lady Elliot Island – southern GBR. Natural vegetation is recovering after nineteenth century guano mining and construction of airstrip in late twentieth century. Photo © QuintonMarais.com 2006.



**Infrastructure and Reef Islands, Figure 4** Dredging to enlarge boat harbor at Heron Island, southern GBR, released silt and mud onto adjacent reef flat. Photo: QNPWS, November 1987, supplied by Department of Environment and Resource Management, Queensland.

a coral cay inevitably also is the location of the largest trees which are the favored nesting sites for some bird species.

Fresh water may have to be imported, collected from rainfall, pumped from underlying fresh water lenses, or obtained by desalination of sea water. In some situations where fresh water is scarce, salt water can be used for some purposes, e.g., flushing toilets and firefighting. In other cases, appropriately treated sewage effluent can be used to water gardens and lawns.

Waste disposal creates problems. For example, at Green Island, the most visited cay on the GBR, sewage used to be discharged onto the reef flat. During a period of more than 30 years of sewage discharge, the area of seagrass on the reef flat expanded from 900 to 130,000 m<sup>2</sup> (Hopley, 1982). These seagrass beds trapped sand eroded from the cay's beaches, preventing its return to the cay and thus contributing to the latter's continuing loss of sand (BPAQ, 1989).

Untreated sewage and agricultural fertilisers from nearby mainland contain high concentrations of nitrogen and phosphorous and these nutrients impose stress upon corals; encourage competition from marine grasses, algae and filter feeders such as sponges; ultimately they weaken the coral leading to its destruction (Bell, 1991; Kinsey, 1991; Rasmussen et al., 1993). Wave-induced groundwater flow from the ocean through atoll islands can transport liquid wastes, originally discharged from dwellings into the island sediments, into the atoll lagoon, resulting in pollution of lagoonal waters (Nielsen, 1999).

Hence, sewage needs to be treated to a high standard of purity before it can be released into atoll lagoons or ocean waters in the vicinity of coral reefs and islands. General waste, particularly on small reef islands, may have to be removed from the islands for disposal elsewhere.

Electric power usually is generated by local diesel power units since solar and wind power do not operate well with large bird populations. On small islands, or in confined areas, diesel generators can create unacceptable noise problems.

Construction of causeways linking atoll islands may result in higher ocean water levels on the seaward side of these islands and stronger currents in the residual channels between them, causing overtopping, erosion and destruction of both islands and causeways. Causeways also block exchange between ocean and lagoon waters, reduce the flushing of a lagoon and hence cause deterioration of water quality in lagoons (Coleman, 1991, Maragos, 1993).

The shoreline alignments of coral cays change with changing wind and wave conditions with the most vulnerable part of the cay being the apparently sheltered lee side.

In the Great Barrier Reef (GBR) region, the tourist resorts on both Heron and Green Islands have required sea defence works, such as groynes and seawalls (Figures 5 and 6), as well as beach replenishment, to protect infrastructure constructed in earlier times on land which was located on the potentially unstable part of the cay (Gourlay, 1983). As on many mainland coasts, such works are not always successful because of their inappropriate nature, inadequate design and lack of environmental information, particularly wave and current data. Moreover, it is essential that designers of such works recognize the unique circulatory nature of the coastal processes operating around small reef islands (Kench et al., 2003). Properly designed coastal engineering works on small reef islands will require relatively more extensive investigations and hence will be more costly than similar works in more benign environments (Gourlay et al., 2004, p. 24).

### Flooding and disaster protection

Reef islands are located in the tropics and those between 10° and 30° latitude are subject to the impact of tropical cyclones (hurricanes, typhoons). All are potentially vulnerable to tsunamis. This means that reef island communities need appropriate disaster management plans.

Low-lying reef islands, such as coral cays, are vulnerable to flooding from storm surges, swells from distant storms and tsunamis. Storm surges are associated with cyclone-generated wind waves and strong winds. Shoreline erosion, destruction of trees and other vegetation, as well as damage to infrastructure, can be expected with a direct hit or near miss cyclone. The risk of this occurring



**Infrastructure and Reef Islands, Figure 5** Seawall constructed at Heron Island, southern GBR, to protect resort buildings from shoreline erosion. Seawall construction, using local materials and cement, began in mid-1950s and is ongoing as required. Photo: Jennifer Hacker, January 1994.





**Infrastructure and Reef Islands, Figure 6** Seawall, designed according to engineering principles using interlocking precast concrete blocks, constructed to prevent shoreline erosion on the leeside of Green Island, northern GBR. Photo: Michael Gourlay, May 2001.

varies in different regions and depends upon the frequency and intensity of cyclones, the tidal range, and the elevation of the islands. Severe tropical cyclones are more likely to occur in latitudes  $15^{\circ}$  to  $20^{\circ}$  than in lower latitudes. Large tidal ranges reduce the risk of flooding from storm surges. Hence, cays within the GBR, where tidal ranges are generally at least 2 m, are less likely to be flooded than the ones in the Caribbean or the central Pacific and Indian Oceans, where tidal ranges are generally significantly less than 1 m. For example, if the peak surge and largest waves occur at low tide in the southern GBR, damage to infrastructure will be caused largely by wind and rain but not by waves. However, if the peak conditions occur at a high spring tide (range ca 3 m), massive destruction of both natural island geomorphology and human infrastructure almost certainly will occur with probable loss of life if prior evacuation of humans has not been possible.

Distant storms, hundreds or even a few thousand kilometers away from a reef island, can generate swells which break on the island's protecting reef causing significant wave set-up, particularly in microtidal environments. On some occasions, the resulting higher water levels and larger waves on the reef top will erode beaches, damage harbor breakwaters and flood settlements on low-lying land behind the reef (see Chapter *Wave Set-Up*).

Tsunamis also may occur under clear skies and without large storm waves or strong winds. Inundation may be total such as that which occurred in the low-lying reef islands of the Maldives in December 2004. Infrastructure damage will occur but loss of life may not be large, if adequate warnings are possible and people can be evacuated to high ground or specially constructed refuge towers or even boats in open water to ride out of the passage of the tsunami. Total inundation of a reef island by storm surge



**Infrastructure and Reef Islands, Figure 7** Raine Island beacon constructed in 1844 on the outer northern GBR, showing erosion of cay rock foundation by nesting turtles. Photo: David Hopley, March 1977.



or tsunami is likely to pollute island freshwater aquifers (Goffredo et al., 2007; Srinivas and Nakagawa, 2008).

### Infrastructure for navigation and weather monitoring

The GBR is the largest system of coral reefs in the world and adjoins a well-populated coastal region, exporting large quantities of minerals and agricultural products. Many ships need to navigate its waters and provision of navigation aids commenced in the middle of the nineteenth century.

Raine Island is the largest cay on the outer reefs of the GBR, located at the entrance to a passage from the Coral Sea to inner GBR waters. The earliest beacon on the GBR was constructed on this island by British sailors and convicts from New South Wales in 1844 using local cay rock (Figure 7). Subsequently, as steamships replaced sailing ships, the sheltered inner passage became the preferred course for shipping, initially sailing in daylight hours and anchoring at night. More navigation aids were needed – unlit wooden beacons and even coconut palms planted on coral cays. As pressure developed for shorter

passage times, together with increasing loss of life from vessels hitting reefs, manned lightships and lighthouses were installed (Figure 8). During the twentieth century, automatic lights progressively replaced manned lightships and lighthouses. Subsequently, in the late twentieth century visible lights were progressively replaced by radar reflecting beacons. All these navigation aids were located in the regions subject to cyclonic winds and waves. Some of them were located on small coral cays or reefs without islands.

During the 1970s, the need for weather forecasting data, particularly for tropical cyclones, led to the establishment of automatic weather stations on various reefs and cays in the Coral Sea eastward of the GBR.

All these structures located on reefs and cays need to be designed and constructed with special consideration of the tropical coral reef environment. Coral cays cannot be relied upon to provide stable platforms for foundations, because of their unstable shorelines (Figure 9). Coral reefs provide a very heterogeneous substrate of hard limestone, softer detrital material and cavities full of coral mud



**Infrastructure and Reef Islands, Figure 8** North Reef Lighthouse, southern GBR. Caisson foundation on reef flat ensures structure's stability as unstable sand cay changes location. Photo: Isobel Bennett, December 1950.



**Infrastructure and Reef Islands, Figure 9** Automatic weather station constructed on Gannet Cay, in Swain Reefs, GBR, has been rebuilt on pile foundations after the original structure's shallow foundations had subsided when the cay changed location. Photo: Peter Flood, early 1980s.

(Hopley, 1991; Simmons, 1991). Sometimes, piles cannot be driven into the reef top; other times, piles do not reach a firm substrate. Raft-type foundations spreading the load over a larger surface area of the reef top have been adopted in many situations, while the most recent new structures are large cylinder caissons located in inter-reefal waters of the continental shelf.

The highly corrosive tropical marine environment requires either the use of expensive corrosion-resistant materials or frequent maintenance and replacement of structures. Furthermore, birds and the guano they produce are likely to interfere with the operation of instruments.

## Conclusion

Special care is required when locating, designing, constructing, and maintaining infrastructure in coral reef regions. Infrastructure located on reefs and unstable reef islands inevitably affects the natural environment and is also affected by the harsh marine environment in these regions. In most cases, the site-specific investigation of the waves, currents and other factors affecting this infrastructure will be complex and hence its cost will comprise a relatively larger proportion of the total project cost compared with similar works located in more benign coastal environments. These low-lying islands and their infrastructure are also vulnerable to flooding from storm surges, wave set-up and tsunamis, as well as rising sea levels.

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## Cross-references

Atoll Islands (Motu)  
 Boat Channel  
 Cay Formation  
 Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity  
 Climate Change: Increasing Storm Activity  
 Coral Cays-Geohydrology  
 Engineering On Coral Reefs With Emphasis On Pacific Reefs  
 Low Wooded Islands  
 Maldives  
 Mangrove Islands  
 Mining/Quarrying of Coral Reefs  
 Reef Structure  
 Tropical Cyclone/Hurricane  
 Tsunami  
 Unvegetated Cays  
 Vegetated Cays  
 Wave Set-Up

## INTERNAL CIRCULATION

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### Synonyms

Pore-water dynamics; Reef framework circulation

### Definition

Internal circulation is the movement of water through the reef framework caused by hydraulic gradients at a range of time and space scales.

### Introduction

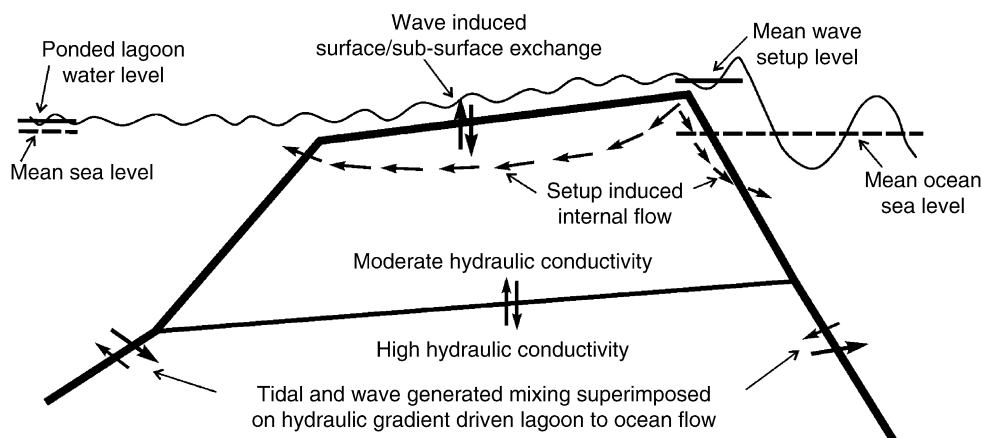
The driving mechanisms, the pathways, and the speeds of water movement through the reef framework are important for reef diagenesis, for the mass transport of solutes (such as nutrients) between the sub-surface (pore) waters, the benthic layer, and the surface waters (with biological and geochemical implications), and for the understanding of coral cay and fringing reef geohydrology (Buddemeier and Oberdorfer, 1988). For laminar flow, Darcy's Law that relates water movement through a homogeneous porous media to the hydraulic gradient and the hydraulic conductivity (primarily a function of permeability) applies. The assumption of laminar flow is likely to hold for all but a few environments, such as in large cavities in the vicinity of breaking waves. Coral reef environments, however, rarely have homogeneous framework at all but the smallest spatial scales, with sometimes extreme differences in both the horizontal and the vertical. Cavities and loose sediments composed of rubble and/or coarse sands exist alongside solid coral heads and densely packed fine sediments, meaning that flows can be variable over very short distances. Advective flows clearly dominate internal circulation, but molecular diffusion, with

diffusion coefficients in the order of  $10^{-10}$ – $10^{-9}$   $\text{ms}^{-2}$  (Li and Gregory, 1974) must also be recognized.

### Driving mechanisms

A model of the principal driving mechanisms for internal circulation is presented by Buddemeier and Oberdorfer (1988) (Figure 1). They also suggest upper limit velocities associated with the various mechanisms, and these are reported in brackets in relation to the various mechanisms in the following discussion.

Hydraulic gradients caused by wave set-up are capable of sustaining uni-directional flows ( $10^{-4}$   $\text{ms}^{-1}$ ) through the reef framework. Wave setup generated hydraulic gradients can be substantial, but will tend to zero under calm wave conditions or at low tide. Although they have the potential to generate significant internal circulation, the zone in which the gradient is highest is frequently highly lithified with a relatively impermeable surface (such as a pavement of crustose coralline algae), which may inhibit the flow of water into the framework. When water is driven by wave processes into the lagoon, ponding may result in a hydraulic gradient, which will cause a net lagoon to ocean flow ( $10^{-5}$ – $10^{-4}$   $\text{ms}^{-1}$ ), suggested by Buddemeier and Oberdorfer (1988) to be preferentially directed through deeper reef framework, and which is suggested by them to be capable of flushing large volumes of high-permeability aquifer on the scale of years to decades. Localized steeper hydraulic gradients may form for short periods, particularly during periods of outgoing tides, causing shallow flows orders of magnitude higher than the long-term ponding-driven flows. Ponding generated flow is superimposed on flows in the framework caused by other regional currents (up to  $10^{-3}$   $\text{ms}^{-1}$ ), including tidal currents ( $10^{-5}$   $\text{ms}^{-1}$ ) normally oscillatory at the tidal period. A current that forces water against the reef can set up a hydraulic gradient in the permeable reef framework capable of driving pore water flow. Density generated gradients caused by evaporation resulting in



**Internal Circulation, Figure 1** The principal driving mechanisms causing internal circulation of water in a reef framework (after Buddemeier and Oberdorfer, 1988).



high salinity water sinking to the seabed ( $10^{-8} \text{ ms}^{-1}$ ), and thermally driven flows ( $10^{-7} \text{ ms}^{-1}$ ) may be present in some situations. Density driven circulation has been described at a large scale by Leclerc et al. (1999).

Groundwater generated hydraulic gradients resulting from recharge of the freshwater lens on reefs with coral cays (see *Coral Cays – Geohydrology*) can generate slow internal flow ( $10^{-7} \text{ ms}^{-1}$ ). However, in some circumstances where the Ghyben-Herzberg model of the freshwater lens applies, water exits the freshwater lens at the island shoreline, resulting in local flows potentially at least an order of magnitude higher. On fringing reefs, or on reefs with other elevated land adjacent (such as raised coral islands), flows within the adjacent reef framework may be orders of magnitude higher (Parnell, 1986) than in the typical coral cay case. Where the tidal range is significant and the reef flat drains, hydraulic gradients can be significantly greater and water speeds within the framework similarly large.

The primary effect of waves, on the other hand, although capable of causing horizontal flows in surface layers, is to provide a pumping mechanism in the vertical, an important process in the mixing of surface waters and shallow pore waters. Buddemeier and Oberdorfer (1988) suggest speeds of up to  $10^{-2} \text{ ms}^{-1}$ . They demonstrate that a 10 s period wave has the potential to move about  $2 \text{ m}^3$  per  $\text{m}^2$  in and out of the reef surface.

Low frequency, high intensity events such as major storms, tectonic movements, and tsunamis can cause pressures resulting in very significant water flows within the framework and within island sediments. For example, there were many accounts of water bubbling up through the reef framework, and water pressure from underneath causing hard tile floors in houses on coral cay islands to buckle during the 2004 Indian Ocean tsunami (Australian Government Mission and the Maldives Marine Research Centre, 2005). Such events may also cause changes to the structure of individual reefs, permanently altering the hydraulics.

## Experimental studies

In separate studies using fluorescent tracers within the Great Barrier Reef Marine Park, Parnell (1986) reported water movement within a fringing reef flat in the order of  $40 \text{ m day}^{-1}$ , and Oberdorfer and Buddemeier (1986) reported flows of between  $0.2 \text{ m day}^{-1}$  and  $400 \text{ m day}^{-1}$  on a mid shelf reef, but generally being in the order of  $10 \text{ m day}^{-1}$ . Both studies recorded considerable vertical movement within the framework. Most water movement resulted from bulk flow through high permeability zones (voids and rubble) with flows in less permeable framework being much slower. Oberdorfer and Buddemeier (1986) comment on the striking similarities in the results of the two studies, despite the considerable differences in the characteristics of the study locations, concluding that the dominant factor was the heterogeneity of reef sediments. The mid-shelf study also demonstrated large fluxes

of water across the reef surface (in the order of  $10\text{--}1,000 \text{ m}^3$  of water per  $\text{m}^2$  per year).

Numerous studies have concentrated on pore water chemistry, showing that transport in the surface layers is higher than at greater depths, possibly indicating the importance of wave and current driven transport (Tribble et al., 1992; Falter and Sansone, 2000). Some studies have shown extremely short residence times in the upper few meters of the reef framework, attributing the results to wave driven oscillations and “stable head differences of uncertain origin” (Tribble et al., 1992, 1290). McCullough and Land (1992) noted the importance of flow through high permeability zones to reef diagenetic processes.

## Summary

A number of processes result in hydraulic gradients that drive internal circulation on coral reefs at a range of time and space scales, including wave setup, lagoon drainage, tides, and other regional currents, density gradients, groundwater flow, and oscillatory waves. Some flows, such as wave driven pore-water circulation can be very fast, resulting in large water turnover between surface and subsurface sediments, over relatively small areas, whereas at the other end of the spectrum, slow flows driven by other mechanisms affect large volumes of framework, over periods extending from years to geologic time. Field studies have indicated flow through reef framework in the order of tens of meters per day, with water moving in high permeability zones such as cavities and rubble dominating bulk flow.

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## Cross-references

[Cay Formation](#)  
[Coral Cays-Geohydrology](#)  
[Diagenesis](#)  
[Hydrodynamics of Coral Reef Systems](#)  
[Lagoons](#)  
[Reef Structure](#)  
[Waves and Wave-Driven Currents](#)  
[Wave Set-Up](#)

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## INTRINSIC AND EXTRINSIC DRIVERS ON CORAL REEFS

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### Synonyms

Autogenic and allogenic drivers on coral reefs

### Introduction

The morbidity and mortality of reef-building corals have increased worldwide in recent decades, resulting in declines of both living coral cover and the density of coral colonies (Gardner et al., 2003; Bruno and Selig, 2007; Wilkinson, 2008; Schutte et al., 2010). Coral populations have not declined uniformly in time or space, and on some reefs they have remained stable or increased (Porter and Meier, 1992; Murdoch and Aronson, 1999; Aronson et al., 2005); nevertheless, the overall downward trend is indisputable. Because there are so many potential drivers of change on coral reefs, assigning causality to observed patterns is difficult. Ecology strives to ascertain the relative importance of multiple processes that are causing change, rather than to falsify individual explanations or classes of explanation (Quinn and Dunham, 1983). The complexity and scale dependence of pattern and process have led to considerable controversy over what is happening to coral reefs.

### Causal typologies

Ecologists have tended to classify stresses, disturbances, and other processes as either intrinsic or extrinsic. Intrinsic and extrinsic causes can be further classified based on whether they are natural or anthropogenic, and the scales at which they operate (local or regional–global). Strict adherence to these typologies has led to confusion over complex cases. The types, intrinsic and extrinsic, natural and anthropogenic, and local and regional–global, are usefully viewed as the endpoints of continua, rather than as specific targets of classification.

Intrinsic drivers act at small, local spatial scales and include processes such as predation, herbivory, competition, recruitment, juvenile mortality, adult mortality, succession, framework accretion, and framework bioerosion. Changes in these processes generate changes

in reef communities. Ecological succession following a disturbance such as a cyclone (an extrinsic disturbance) would appear to be a clear example of a natural, localized, intrinsic process in coral reef communities. The upward vertical accretion of a reef, which is based on coral growth, raises the living community into shallower water, so in the absence of changes in sea level, the shallowing-upward replacement sequence of corals should be considered autogenic succession (Aronson et al., 1998). (In contrast, reef drowning from rapid sea-level rise, which results in a deepening-upward sequence, is extrinsically driven.) Even succession, however, is not without its classificatory problems. The trajectories of successional sequences will vary in accordance with varying regimes of extrinsic disturbances such as cyclonic activity and global change (Connell, 1978; Done, 1999).

Extrinsic drivers of change on coral reefs include local anthropogenic stresses such as pollution, sedimentation, and nutrient loading (eutrophication); local anthropogenic disturbances such as ship groundings, coral mining, and blast fishing; local natural stresses such as upwelling and the off-platform transport of hot/hypersaline or cold/hyposaline, inimical waters; local natural disturbances such as bioerosion, coral mortality caused by damselfish (Pomacentridae) and other corallivores, tectonic activity, and lava flows; large-scale natural stresses such as increased turbidity following heavy rains and variations in insolation; large-scale anthropogenic stresses such as global warming and ocean acidification; large-scale natural disturbances such as regional disease epidemics of corals and herbivorous echinoids, interruptions in connectivity (i.e., larval supply), and regional outbreaks of the corallivorous seaster *Acanthaster planci*; and large-scale anthropogenic disturbances such as introductions of alien species, increased turbidity from large-scale deforestation, and pan-tropical overfishing. The limited utility of these simplistic classifications for science and management is highlighted by the example of perturbations to larval supply, which can be natural or anthropogenic, and which can act on local to regional spatial scales (Sammarco, 1985; Hughes et al., 2002). Overfishing is clearly anthropogenic, but it can be viewed as a local, regional, or global source of disturbance, and it is extrinsic or intrinsic depending on whether or not human fishers are considered part of the reef ecosystem.

### Evolving models of reef dynamics

Despite these difficulties, broad generalizations are possible about intrinsic and extrinsic drivers of reef dynamics. One widely accepted scenario for the Caribbean region emphasizes the role of human predation in causing degradation of reefs in the 1980s and 1990s. Historical overfishing reduced populations of herbivorous fishes, and then in 1983–1984 a regional disease outbreak decimated the ecologically important echinoid *Diadema antillarum*, with the cascading consequence that declining herbivory released fleshy and frondose macroalgae

(seaweeds) to overgrow corals and dominate reefs (Jackson et al., 2001). This is a hypothesis about local, intrinsic processes responding to extrinsic disturbances (if fishing is considered extrinsic). The scenario is incorrect in this strict form because (1) direct observations showed macroalgal overgrowth of corals to have made a minor contribution to reef degradation (Aronson and Precht, 2006) and (2) contrary to popular opinion among coral reef scientists, the majority of Caribbean reefs are not dominated by macroalgae (Bruno et al., 2009). In a modified version, extrinsic disturbances such as cyclones, which kill corals and open space for algal colonization, interacted with overfishing of herbivores and the loss of *Diadema* to promote a macroalgae-dominated state (Hughes, 1994). This version is also not entirely correct, because sufficient levels of coral mortality can lead to macroalgal dominance even without reductions of herbivores (Ostrander et al., 2000; Williams et al., 2001). In such instances, widespread coral mortality overwhelms the capacity of populations of herbivores to respond sufficiently to forestall macroalgal dominance.

More realistic scenarios of reef degradation emphasize the primary (but not exclusive) role of extrinsic factors, especially infectious coral diseases, thermally induced coral bleaching, and their interactors, in causing coral mortality, with or without ensuing shifts to macroalgal dominance (Hoegh-Guldberg, 1999; Aronson and Precht, 2001, 2006; Hughes et al., 2003). Even remote, quasi-pristine reefs in the Indo-Pacific have been affected by temperature-induced bleaching (Alling et al., 2007; Sandin et al., 2008), emphasizing the now-overriding importance of large-scale, extrinsic influences related to human activities, especially climate change. Intensifying ocean acidification and rising eustatic sea levels are additional, extrinsic effects of climate change that likely will have negative impacts on coral populations in the not-too-distant future (Kleypas et al., 1999; WBGU 2006; Hoegh-Guldberg et al., 2007).

Nutrient loading, whether viewed as intrinsic or extrinsic, appears to be a relatively minor driver of coral and algal dynamics in most cases (Hughes et al., 1999; Aronson and Precht, 2000), but the relationship between top-down consumption (predation and herbivory) and bottom-up, nutrient-driven production is complex (Burkepile and Hay, 2006; Littler et al., 2006). The new consensus on (reduced) herbivory is that its contribution to algal dominance was overstated; however, by controlling macroalgae, herbivorous fish and echinoids can facilitate the recruitment and recovery of coral populations (Bythell et al., 2000; Hughes et al., 2003; Carpenter and Edmunds, 2006; Idjadi et al., 2006; Birrell et al., 2008; Mumby and Harborne, 2010).

## Summary

Coral populations and their recovery from stresses and disturbances will continue to be driven by combinations of factors, but categorizing them as intrinsic or extrinsic

is not as useful as understanding the scales on which they operate. The process or interaction of processes that exerts the strongest influence will by logical necessity be the limiting factor to corals. Addressing regional and global problems such as greenhouse-gas emissions and species introductions will leave local factors to limit coral populations, and vice versa. Simultaneous action on anthropogenic drivers at multiple scales is the only way to mitigate and, hopefully, reverse the degradation of coral reefs.

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## Cross-references

[Acanthaster planci](#)  
[Algae-Macro](#)  
[Bioerosion](#)  
[Climate Change and Coral Reefs](#)  
[Historical Ecology of Coral Reefs](#)  
[Impacts of Sediment on Coral Reefs](#)  
[Nutrient Pollution/Eutrophication](#)  
[Ocean Acidification, Effects on Calcification](#)  
[Reef Interconnectivity/Larval Dispersal](#)  
[Sea Level Change and Its Effect on Reef Growth](#)  
[Temperature Change: Bleaching](#)  
[Volcanic Disturbances and Coral Reefs](#)  
[Western Atlantic/Caribbean, Coral Reefs](#)

## LAGOON CIRCULATION

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### Synonyms

Atoll lagoon; Backreef lagoon

### Definition

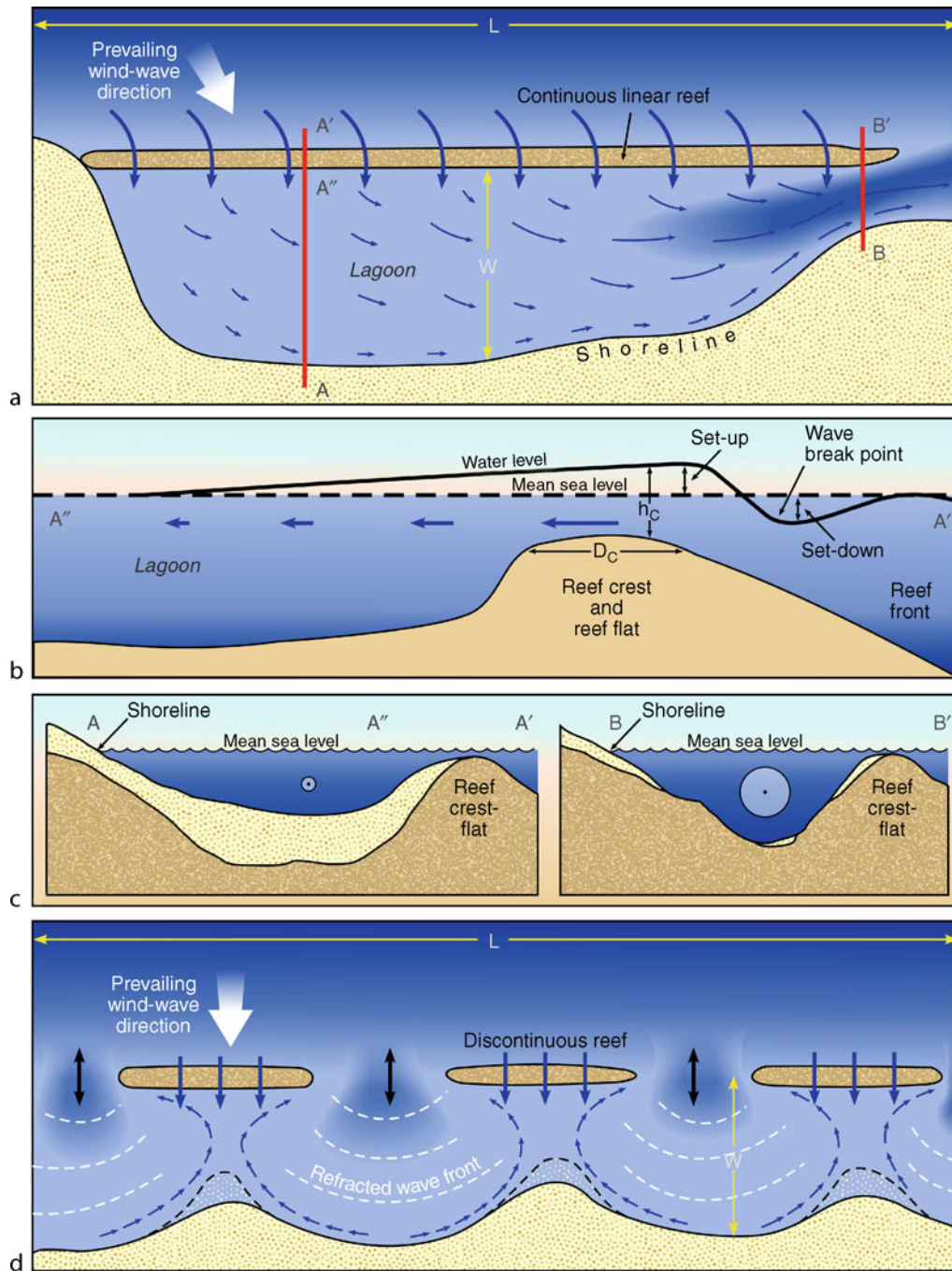
A lagoon is a shallow and generally elongate body of water parallel to the coastline and separated from the open sea by a natural barrier. In siliciclastic sediment systems, this barrier is usually a barrier island, but in carbonate systems, the barrier consists of islands such as the Florida Keys, or more frequently, the barrier is a coral-algal reef of the fringing or barrier type. With atolls, the lagoons can be quite deep and generally circular instead of elongated, and may or may not be associated with a land mass.

### Fringing and barrier reef lagoons

Water circulation in carbonate lagoons is a product of many variables including lagoon dimensions, continuity of the reef barrier, wind speed and direction, wave-swell height and direction, tides, and, to a lesser extent, salinity and water temperature variations. Large-scale ocean currents and high-energy events may also contribute to across-the-reef flow and lagoon circulation (e.g., Coronado et al., 2007). The relevance of each force depends on the interplay between its strength and duration (e.g., wave height, tidal range, and wind speed), reef geometry (water depth and width of the reef crest-flat, and bottom roughness), and the morphology and openness of the lagoon. Figure 1 schematically illustrates two

end-member types of shallow, reef-fronted lagoons where the length of the lagoon ( $L$ ) is usually less than 10–15 km but can extend up to hundreds of kilometers alongshore, such as Ningaloo reef of Western Australia (Hearn and Parker, 1988), while lagoon width ( $W$ ) is generally less than a kilometer or two. These dimensions are typical of fringing reef lagoons both in the Atlantic – Caribbean and in Pacific reef provinces. The reef crest-flat depth  $h_c$  (Figure 1b) affects the way tides, waves, winds, and storm surge interact with the reef (Gourlay, 1994), and the reef crest-flat width ( $D_c$ ), another relevant aspect of reef geometry, also has an impact on wave setup and across-the-reef flow (Symonds et al., 1995; Massel and Brinkman, 2001; Figure 1b). The wider the reef crest-flat (large  $D_c$ ), the more attenuation of cross-reef current velocities and flux into the backreef lagoon.

One reef-lagoon type is characterized by a rather continuous reef with no major breaks. Except in areas where salinities are reduced by freshwater runoff entering the lagoon (Tamura et al., 2007) or in locales where hypersaline conditions develop because of extremely high evaporation rates, e.g., Red Sea (e.g., Friedman, 1968) or Arabian Gulf (e.g., Gunatilaka et al., 1984), waters in fringing reef lagoons are well mixed, have short flushing times (hours–few days, e.g., Hearn and Parker, 1988), and have rather simple circulation patterns. Flow into the lagoon shown in Figure 1a is primarily from water-level setup and overtopping associated with wave breaking on the reef front or crest. The resulting water-level gradient between the reef front and backreef lagoon drives a net flux of ocean water lagoonward. Wave setup in submerged reefs ( $h_c > 0$ ) is approximately 50% of  $H_0$  when  $h_c < 0.7H_0$  but ~10% of  $H_0$  when  $h_c > H_0$  where  $H_0$  represents the off-reef or incident wave height (Gourlay, 1993; Gourlay, 1996a). However, when  $H_0 < 0.4 h_c$ , there is no setup (Gourlay, 1996b). Figure 1b illustrates wave setup on the reef front and the water-level gradient into



**Lagoon Circulation, Figure 1** (a) A shallow lagoon separated from the open ocean by a continuous reef over which water is driven by prevailing waves and wind. Reef-lagoon system length is  $L$  and lagoon width is  $W$ . Where  $W$  is small, a shore-parallel current develops and accelerates toward the lagoon outlet. (b) A cross section of the reef defined in panel A as profile A'-A'' illustrates water-level setup over the reef crest-reef flat as a product of wave breaking. Width of the reef crest-reef flat is defined as  $D_c$  and water depth over the reef crest-reef flat is  $h_c$ . (c) Cross sections A-A' and B-B' of the lagoon shown in panel A illustrate the effect of increasing current velocities on sediment accumulation in the lagoon. Sediment is stored in the low energy part of the lagoon (A-A') but is transported out of the lagoon leaving the exposed lagoon floor where current velocities are strongest at the point of exiting the lagoon (B-B'). Circles in the lagoon on these cross sections represent the relative speed of currents flowing toward the reader and out of the lagoon. (d) This shallow reef type has a discontinuous reef paralleling a backreef shoreline. Tidal currents and refracted waves traveling through gaps between the reef segments interact with the shoreline to create circulation cells that drive sediments into cusped shoreline features. As lagoon width ( $W$ ) increases along with water depth in the lagoon, these circulation cells break down and lagoon circulation is driven primarily by winds and tides.



the backreef lagoon. The early study of Bikini Atoll in the Pacific Ocean by Munk and Sargent (1948) illustrated that waves breaking on the reef drove strong currents (0.25–0.5 m/s) that transported water over the reef and into the lagoon. In a fringing reef setting in the Caribbean, Roberts and Suhayda (1983) measured strong short duration cross-reef currents of >0.4 to 1.8 m/s. Cross-reef currents and volume flux change with the tide. Maximum flux occurs at high tide, but during very low tides (extreme neap tides) and/or off-reef winds, currents may be reversed and water may flow off-reef from the lagoon. Cross-reef flux estimates range from 0.01 to 2.21 m<sup>2</sup>/s (Marsh et al., 1981; Pickard, 1986; Lugo-Fernández et al., 1998, 2004; Gourlay and Colleter, 2005). Wave-driven flows contribute about 45–60% of the total flow in some Pacific and Caribbean reefs (Pickard, 1986; Lugo-Fernández et al., 2004). The remainder of the flow can be attributed to tides, wind stress, and infragravity waves (Lugo-Fernández et al., 1998).

Because of their small amplitudes and long wavelengths or periods (24 and 12 h), the astronomical tides behave as shallow waters waves, the velocities of which depend on amplitude and water depth. Tidal currents reverse direction once or twice a day affecting across-the-reef flow into the lagoon through surge channels and/or larger tidal channels. These linked processes are well established for barrier reef lagoons and especially atoll lagoons where tides impinge unaffected on them from deepwater. If the tidal amplitude is large enough to expose the reef crest-flat, then at low tide water-level gradient will develop that drives an off-reef flux, which depends on the degree of connectivity between the lagoon and adjacent ocean (Yamamoto et al., 1998). Infragravity waves are other shallow waves affecting cross-reef currents. These flows have not been well studied, but have been observed on shelves with reefs (Roberts and Suhayda, 1983; Wolanski, 1994; Lugo-Fernández et al., 1998).

Strong winds either reinforce or oppose the wave- and tidal-driven flows depending on wind direction. In fringing reefs, these effects are accentuated because of the small water depths and the accumulation of water against the coast, which creates a pressure gradient that opposes all inflow at the reef crest. Under such conditions, a two-layer flow may develop if the lagoon is large enough and deep enough to accommodate such a two-layer system, on-reef flow at the surface and off-reef flow near the bottom (Storlazzi et al., 2004). As lagoon–land geometries become more complex and scales increase ( $W$  and  $L$ ) over-the-reef flow becomes less important for driving lagoon circulation. As in the case of the Great Barrier Reef Lagoon near Lizard Island, Frith and Mason (1986) found that circulation was highly coherent with the trade wind for about half the year, but exhibited much more variability (e.g., current reversals) after the trade wind season ended. Wind shifts and tides accounted for this lagoon circulation variability.

Recently, Monismith et al. (2006) describe a cross-reef flux driven by buoyancy created by temperature

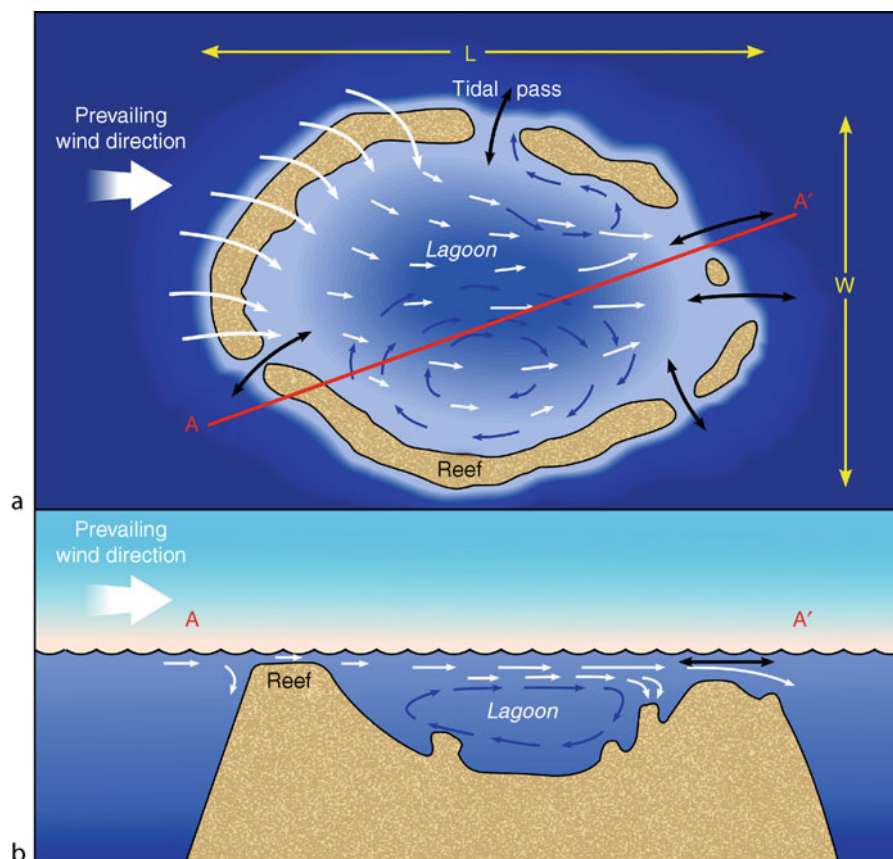
differences between the outer reef and lagoon. A similar buoyancy flux should operate on reefs with hypersaline lagoons. Hypersaline conditions are prevalent throughout the reef-lagoon systems of the Red Sea (e.g., Friedman, 1968; Meshal, 1987) and the Arabian Gulf (e.g., Kinsman, 1969; Gunatilaka et al., 1984) because of excessive evaporation.

Inside the lagoon, cross-reef flows, tides, and winds drive a circulation which is constrained by the lagoon's morphology. Figures 1a and 2 illustrate different shallow reef-lagoon geometries and their effects on the lagoon circulation. In the case of a backreef lagoon with limited connectivity with the open ocean, a small width, and a shallow depth, the flow is generally downwind and tends to accelerate as the lagoon outlet is approached (e.g., Roberts, 1980; Tamura et al., 2007; Figure 1). If the reef fronting a shallow lagoon is discontinuous as schematically illustrated in Figure 2, localized circulation cells may develop. Such cells are primarily a product of shoreline currents created by waves refracted through openings between reef segments. These divergent currents at the shoreline create cusped shoreline morphologies. However, when  $W$  increases to beyond narrow fringing reef-lagoon barrier reef scale, these circulation cells break down and lagoon circulation becomes wind- and tide-dominated (as described by Wolanski, 1994).

### Atoll lagoons

Atolls are a special type of reef-lagoon system. Early in the study of oceanic processes and their impacts on reefs and their lagoons, von Arx (1948) conducted a groundbreaking study on lagoon circulation at Bikini and Rongelap Atolls. Circulation in both lagoons was primarily wind-driven in the surface layer with overturning and counter-rotating cells established in the deeper parts of the lagoons. This two-layer flow is illustrated schematically in Figure 2. Strength of both surface and deeper layer circulation was found to vary over a day with changing wind speed. Smaller variations were found to be related to perturbations caused by wave-swell environments, tides, and changes in major ocean currents encountering the atolls. At both Rongelap and Bikini Atolls, over 2% of the lagoon volume was found to be transported into and out of the lagoons on each tidal cycle.

Like their fringing reef and barrier reef counterparts, over-the-reef flux of ocean water to the atoll lagoon is driven by a water-level gradient established primarily by the breaking of waves on the reef front. Atolls located in monsoonal regions, such as the Maldives in the Indian Ocean, receive winds and waves from two dominant directions. It follows that lagoon circulation reversals will occur at the monsoon frequency. An investigation of Cocos (Keeling) islands by Kench (1994), an Indian Ocean Atoll with a lagoon about 3–5 km diameter, determined that atoll structure controlled the pattern of energy distribution and lagoon circulation. In this case, tidal currents drove lagoon circulation and water had a residence



**Lagoon Circulation, Figure 2** (a) A schematic plan view representation of two-layer circulation in an atoll lagoon. White arrows represent surface currents, blue arrows are deep counter currents, and black arrows are tidal currents concentrated in the tidal passes. (b) This cross-sectional view of the atoll lagoon along line A–A' in panel A shows the surface current (white arrows) forced by wave-driven cross-reef flow plus wind stress and a counter current in the deep part of the lagoon.

time of 2–5 days. Wave- and tide-driven flows through shallow reef channels were important to ocean–lagoon exchange, but along with wind were found to be less important than tidal exchange as a driver of lagoon circulation. In the case of atoll-like platform reefs, such as One Tree Reef of the Southern Great Barrier Reef, lagoon water may be ponded behind the high rims of the platform and may be largely isolated from oceanic energy (tides and waves) that drives circulation in most reef lagoons (Ludington, 1979; Frith and Mason, 1986).

### Summary

Coral reef lagoons span a wide spectrum from small nearly closed to large and open lagoons in atolls. Water circulation in these lagoons results from the strength and duration of driving forces (e.g., wind speed and direction, wave-swell height and direction, tides, major currents, and salinity and water temperature variations) and their interaction with the morphology and geometry of the lagoon. In small nearly closed lagoons, currents are directed nearly parallel to the coastline because of the morphological and geometric constraints under the action of waves, tides, and winds.

As the size and openness of the lagoon increases, winds and tides become the dominant forces of water circulation. In large lagoons of atolls, winds and tides are the primary forces of circulation assisted by the wave driven across the reef flux. However, because these lagoons are much deeper, water stratification becomes relevant and two-layer flows are common.

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## Cross-references

Atolls  
 Hydrodynamics of Coral Reef Systems  
 Lagoons  
 Sediment Dynamics  
 Tidal Effects on Coral Reefs  
 Wave Set-Up  
 Waves and Wave-Driven Currents

## LAGOONS

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Fully or partly enclosed depressions in coral reefs are common. They range in depth from 1 or 2 m to > 90 m with the largest occurring in atolls, e.g., Kwajalein (Marshall Islands) 120 × 32 km or Rangiroa (Tuamotu) 79 × 34 km. They have many origins including the following:

- Shallow moats behind reef flat rubble banks
- “Boat channels” a few metres deep behind a fringing reef attached to the shore
- Deeper lagoons behind reefal rims around volcanic islands as in the Darwinian sequence
- Shelf reef lagoons of probable karst inheritance (Purdy, 1974) but with some Holocene growth to the rim (see *Reef Classification by Hopley (1982)*). These reefs and their lagoons can be > 100 km<sup>2</sup> in area (e.g., Hopley, 2006)
- Extensive lagoons of atolls some of which may be entirely closed off from the ocean. Purdy and Winterer (2001) have shown that only about 10 m of lagoon rim relief in these largest of lagoons (> 250 km<sup>2</sup>) is the result of reef growth, the remainder (> 20 m) is due to dissolution over several glacial/interglacial cycles and only a small amount due to subsidence
- Depressions resembling karst but originating from the rapid *Acropora* dominated growth (> 6 m/ka) from patch and reticulated foundations and including collapse of depression walls (Wyrwoll et al., 2006)

All types are sediment sinks and for fringing reefs terrigenous sediments may dominate the lagoon floor. In terms of



hydrography, lagoons can be divided into three classes, normal, brackish, and hypersaline, which combined with circulation, can exert a major influence on the sedimentological characteristics of the lagoon (Milliman, 1974). Normal lagoons display temperatures and salinities similar to those of the adjacent ocean. In brackish lagoons, freshwater influx from run-off and rainfall exceeds evaporation: the opposite is true of hypersaline lagoons.

Away from the land masses, lagoon sediments are totally calcareous (apart from a few diatoms and sponge spicules). Corals are common throughout apart from that in deeper lagoons below the level of coral and algal growth where black muds may dominate. Calcareous algae and shell fragments from gastropods, echinoderms, crustaceans, etc. may also be found in all parts of the lagoon but foraminifera tend to dominate shallow waters and *Halimeda* deeper zones beyond 50 m (Guilcher, 1988).

Studies of lagoon infill (e.g., Davies and Hopley, 1983; Purdy and Gischler, 2005) show that once reefs reached sea level at the end of the Holocene transgression, lateral movement of sediment becomes a dominant process, with infill rates of up to 8 m/ka. Occasional high energy storms produce rates up to 18 m/ka. Lagoons in smaller platform reefs may have totally infilled during the Holocene (Hopley et al., 2007). However, as Purdy and Gischler (2005) have shown for large atoll scale lagoons, the extent of Holocene high stand lagoon filling may be minimal. Lateral infilling also comes from patch reef growth, the modal rate of which may be 8 m/ka which once the reef is at sea level also reverts into lagoon infilling in the form of a sediment halo around the patch reef. Although, current speeds, within lagoons are normally low, some sediment movement may take place with the help of bioturbation (Frith, 1983).

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## Cross-references

Atolls  
 Blue Hole  
 Boat Channel  
 Faroes Reefs  
 Lagoon Circulation  
 Moating  
 Moats  
 Reef Classification by Hopley (1982)  
 Residence Time  
 Reticulated Reefs

## LAST GLACIAL INTERSTADIALS

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## Definition

Relatively warm periods recorded in Greenland ice cores during the last glacial.

Last glacial interstadials are strongly related to ocean circulation changes resulting from partial collapsing of continental ice. Sea-level changes also occurred. Ice cores obtained from deep drilling in Greenland by international collaborative efforts have revealed a detailed history of paleoclimates. One of the important discoveries from the ice cores was the identification of abrupt shifts in climate, in particular during the last glacial. Shifts in Greenland surface-air temperature were abrupt changing from cold status to warm status by as much as 10–15°C in decadal time scales or less. This had been previously found in the interval between 20,000 and 75,000 years ago (e.g., Dansgaard et al., 1982; Johnsen et al., 1972, 1992). In the meantime, deep-sea cores were also analyzed and indicated similar millennial scale oscillations. There are two types of rapid climate change according to detailed examinations of the ice and marine cores, namely Dansgaard-Oeschger (D–O) events and Heinrich events (HE). The former has approximately 1,500 year cycles (e.g., NGRIP Members, 2004) whereas the latter appeared every ca. 7,000 years (Yokoyama et al., 2001a; Clark et al., 2007). HE were discovered from sedimentological analyses in the North Atlantic as was noted from the synchronous

appearance of ice rafted detritus (IRD) from deep-sea cores (Heinrich, 1988). This had been recurring when the Greenland surface temperature was at its coldest (Alley, 1998). Distribution patterns of the ice rafted detritus (IRD) in the cores indicated that the Laurentide ice sheet and the ice sheets around the Nordic Seas are the main contributors for releasing icebergs (Heinrich, 1988; Bond et al., 1993; Bond and Lotti, 1995; Hemming, 2004), which melted around 45 degrees north to release freshwater. This impacted on the intensity of Atlantic Meridional Overturning Circulation (AMOC) through the decrease of the North Atlantic Deep Water (NADW) formation. Several paleoceanographic studies showed that the AMOC during a HE nearly ceased and cold climate resulted in the North Atlantic region as was followed by rapid warm D–O interstadials found in Greenland ice cores. During a cold D–O stadial, most of the northern Hemisphere experienced cold climate conditions. The magnitude of sea-level rise associated with each HE has been estimated from 10 to 30 m (Yokoyama et al., 2001a, b; Siddall et al., 2003) and the style of reef development was unique (“pack-up”; Esat and Yokoyama, 2006) compared with traditional three types categorized as “keep-up,” “catch-up,” and “give-up” types depending on the corresponding sea-level changes (Neuman and Macintyre, 1985). The strength of AMOC during a HE was clearly recorded as levels of radiocarbon in corals (Yokoyama et al., 2000, 2001a, 2008). Therefore, frequent but less extensive ice sheet collapses have been repeated and was probably triggering the reduction of NADW formations, but AMOC would still have operated (Ganopolski and Rahmstorf, 2001). The inception and propagation of HEs have been proposed previously (e.g., Hemming, 2004; Clark et al., 2007) including internal oscillations of ice sheet (MacAyeal, 1993; Papa et al., 2006), growth and decay of ice shelf (Hulbe et al., 2004; Alley et al., 2006), and oceanic system dictating mechanisms (Flückiger et al., 2006). Whatever, the key region for creating these abrupt climate changes is the North Atlantic cryosphere-ocean system. Coral reef development during last glacial interstadials and stadials is reported from rapidly uplifted regions such as the Huon Peninsula, Papua New Guinea (Yokoyama et al., 2001; Chappell et al., 1996), and Vanuatu (Cabioch and Ayliffe, 2001).

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## Cross-references

Climate Change and Coral Reefs  
 Emerged Reefs  
 Glacial Control Hypothesis  
 Huon Peninsula, P.N.G.  
 Last Glacial Interstadials  
 Meltwater Pulses  
 Paleoclimate from Corals  
 Postglacial Transgression  
 Reef Classification, Response to Sea Level Rise  
 Sea Level Change and Its Effect on Reef Growth  
 Submerged Reefs

## LAST GLACIAL LOWSTAND AND SHELF EXPOSURE

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### Definition

Occurred at the Last Glacial Maximum (19,000–30,000 years ago) when sea level was lowered globally to as much as 120–130 m.

Last Glacial Maximum (LGM) is the time when global temperature was significantly lower than that of the present and ice sheets covered large areas of northern hemisphere continents. The conventional definition of the LGM was made by an international research project group in the 1980s (e.g., CLIMAP Project Members, 1981) as was the time when low-latitude ocean temperature was at its minimum. However, recent advances of paleoclimate study show that the timing of the LGM is varied depending on the locations on the Earth's surface. Therefore, the most recent date of the “global” LGM is defined as the time when the global ice volume was at its maximum and sea level was at its lowest (Mix et al., 2001). There had been various estimates of the exact levels of sea-level lowstand. Nakada and Lambeck (1988) and Fleming et al. (1998) reviewed published sea-level observations obtained from the sites far from former ice-covered regions. They conducted corrections of glacio-hydro-isostatic adjustments of solid earth (GIA) and concluded that the LGM sea level was 125–130 m lower than the present. Corals obtained from Barbados provided the last 18,000 years of sea-level record and it led to the conclusion that this level may have been 120 m lower than

the present (Fairbanks, 1989; Bard et al., 1990). On the other hand, others claimed that the LGM level may have been only ~105 m (Peltier, 1994). Thus there were large discrepancies for estimates of the sea level at the lowstand during the last glacial.

The Australian continental shelf was targeted to tackle this problem since it is located far from formerly glaciated regions, hence expected GIA is minimal and those corrections are not sensitive to the ice-loading geometry. The continental margins are tectonically stable as was supported by the elevation of the last interglacial shorelines close to the present day sea level (Marshall and Thom, 1976; Stirling et al., 1998). Ferland et al. (1995) worked off Sydney using vibro-cores and concluded that the shelf was exposed during the last glacial lowstand shallower than –130 m. The high-energy sedimentary environments prohibited further refinements. The north-western shelf of Australia, on the other hand, is suited for studying sea-level lowstand since the area is characterized by shallow and wide depressions and hence the conditions may have been favorable for the preservation of former sea-level indicators (van Andel and Veevers, 1967; Yokoyama et al., 2000, 2001a). A series of gravity and vibro-cores were recovered and micropaleontological study with detailed radiocarbon dating shows that the LGM sea level locally reached at 125+/-4 m at least between 22,000 and 19,000 years B.P. and the LGM was terminated rapidly 19,000 years ago when approximately 10% of ice volume decreased. This probably created a ca. 10–15 m rise in sea level (Yokoyama et al., 2000, 2001a). Local sea-level lowstands can be translated into the so-called ice volume equivalent sea level, as much as 135 m (Yokoyama et al., 2000; Lambeck et al., 2002), which can be obtained after GIA corrections. This was the first observation, which extended back into the middle of the LGM, and the GIA-corrected Barbados record was consistent with the northwestern shelf result (Yokoyama et al., 2000). This quantity was further supported by independent studies such as detailed microfossil examinations (De Deckker and Yokoyama, 2009), GIA model (Milne et al., 2002; Mitrovica, 2003), and the Sunda Shelf record (Hanebuth et al., 2000, 2009). Predicted relative sea-level values are available around the Australian continent (Yokoyama et al., 2001b) and the model predictions are confirmed from occurrence of ooids from the Great Barrier Reef, where this part of the shelf was also exposed during the lowstand (Yokoyama et al., 2006). Various impacts from such a lowstand on coral reef formations are still under debate, since there are only a few LGM coral observations so far reported. Coral samples obtained from deep-sea drilling currently being undertaken will allow us to understand the mechanisms on this topic.

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## Cross-references

Barbados  
 Glacial Control Hypothesis  
 Glacio-Hydro Isostasy  
 Great Barrier Reef: Origin, Evolution, and Modern Development  
 Last Glacial Interstadials  
 Last Interglacial and Reef Development  
 Postglacial Transgression  
 Sea Level Change and Its Effect on Reef Growth  
 Submerged Reefs

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## LAST INTERGLACIAL AND REEF DEVELOPMENT

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## Introduction

The last Interglaciation (LIG), defined by half-peak heights in the marine oxygen isotope record, is centered around 125 ka ago and was the last time global ice-volume was at a minimum and sea levels were higher than present (Martinson et al., 1987). The highstand of sea level (SL), which occurred within the LIG, correlates with marine isotope stage (MIS) 5e and overlaps with warm terrestrial stages such as the Eemian, Sangamonian, and Ipswichian (Shackleton et al., 2003). The precise timing of the highstand is based on radiometric dating of SL indicators such as fossil-reef corals and speleothems in stable areas, but there is still uncertainty regarding the reliability of its bounding ages (Edwards et al., 1987; Chen et al., 1991; Szabo et al., 1994; Stirling et al., 1998; Esat et al., 1999; but see Cheng et al., 2009).

In terms of climate, the LIG highstand was a time of unprecedented warmth which led to significant northward expansion of temperate biota. Animals such as hippopotamus were recorded in central and northern Europe for the first and perhaps only time in the last 500 ka (e.g., Schreve, 2009). These dramatic shifts in biota largely resulted from the polar amplification of warming. In the Northern Hemisphere, average summer insolation was 11% above the present between 130 and 127 ka (CAPE, 2006). This led to a rapid, early deglaciation and intensification of Atlantic meridional overturning circulation, which combined to melt sea-ice, permafrost, and almost all glaciers, allowing a vast expansion of the boreal forest to the shores of the Arctic Ocean (CAPE, 2006). The positive feedback resulting from vegetation-induced changes in albedo amplified Arctic summer temperatures, which climbed to an average of 5° above the present (Chapin et al., 2005). Such high temperatures led to the complete disappearance of the south dome of the Greenland ice sheet and to a loss of almost half of its present-day volume, leading to significantly higher SL (Cuffey and Marshall, 2000; Otto-Bliesner et al., 2006).

These elevated temperatures, together with the smaller latitudinal temperature gradient, also led to more

widespread reef development than present, and reefs not only extended further into coastal lowlands but significantly expanded their latitudinal range (Kendrick et al., 1991; Greenstein and Pandolfi, 2008; McCulloch and Mortimer, 2008). The elevation and age of fossil reef-crests from tectonically stable terrains in several areas of the world indicate that the sea level was 3 m higher than the present by ~125 ka and peaked at 6 m sometime thereafter (Stirling et al., 1998; Blanchon et al., 2009).

Reef development during the LIG has played a particularly important role in understanding the causes of climate and sea-level oscillations during glacial–interglacial cycles. First, the absolute timing and duration of reef development has been used to test the Milankovitch theory of orbital forcing, which holds that variation in northern-hemisphere summer insolation drives ice-sheet growth and decay as reflected in SL records (Hays et al., 1976). Second, the age and elevation of fossil reef-crests allow the reconstruction of a high-resolution record of ice-volume and sea level during the highstand, and thus provides an analog for ice-sheet stability in the present interglacial under sustained, greenhouse-gas induced global warming.

### Reef development in uplifted terrains

Reef development in uplifted areas can potentially provide an assessment of the timing of postglacial sea-level rise (or glacial termination) and the duration of the interglacial but, due to the tectonic overprint and the possibility of coseismic displacement, it is difficult to infer anything about the detailed SL behavior or the absolute elevation reached during the highstand.

### Barbados

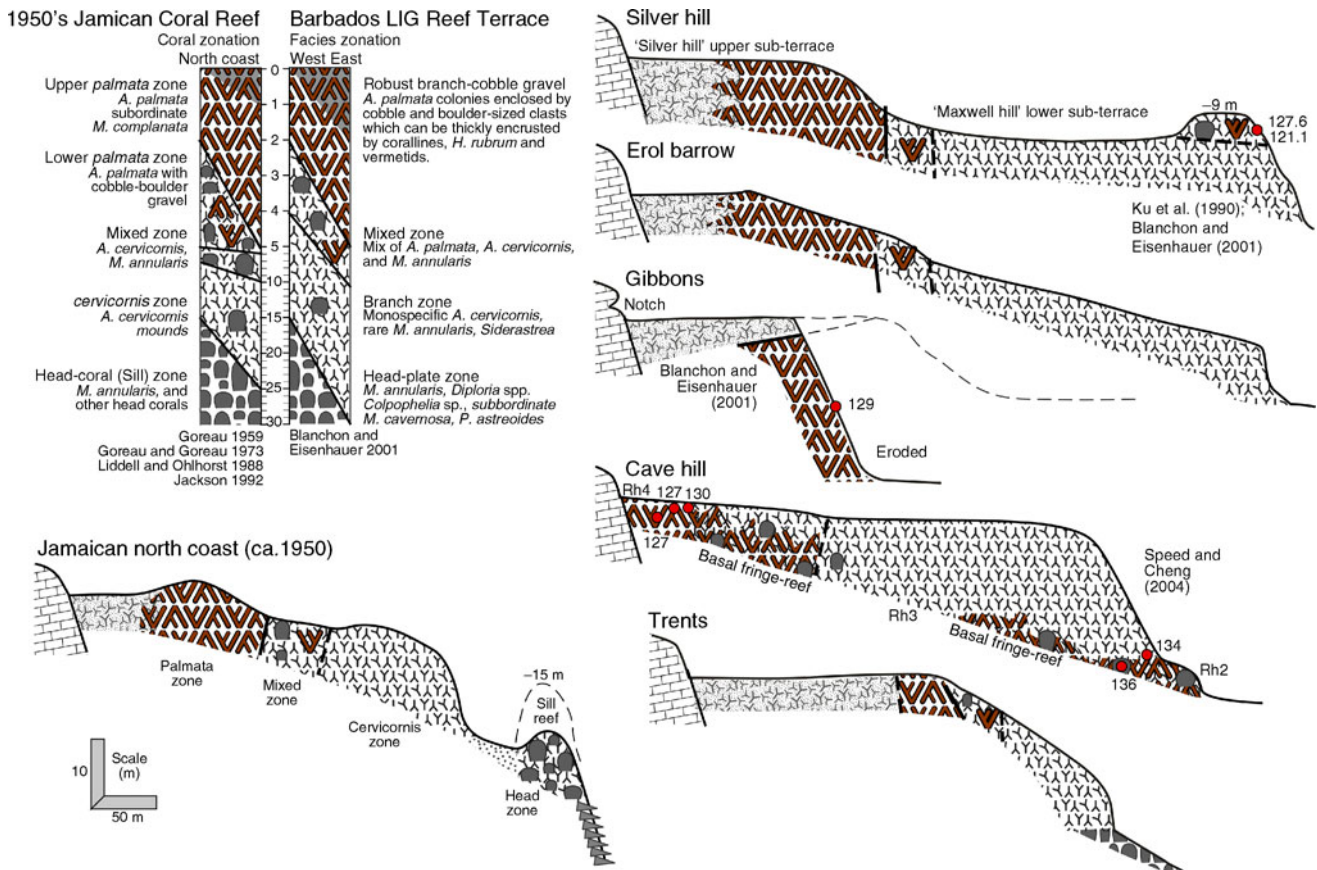
Pleistocene reef terraces on Barbados have been extensively dated by various methods since the late 1960s, and 15 separate terraces have been identified which represent an episodic record of reef development from 640 to 60 ka (Broecker et al., 1968; Meselella et al., 1969; James et al., 1971; Matthews, 1973; Bender et al., 1979). The continuous uplift of the island at rates of up to 0.53 mm/year has produced terraces that record the last six or seven interglacial SL highstands, corresponding to MIS 5–17 (Shackleton and Matthews, 1977; Fairbanks and Matthews, 1978; Taylor and Mann, 1991; Speed and Cheng, 2004).

Early reconnaissance mapping by Meselella and coworkers discovered that many of the interglacial terraces on Barbados displayed a regular, depth-related facies sequence consisting of a deep head-coral zone which passed vertically into thickets of branching *Acropora cervicornis*, and then into the more robust *A. palmata* in the reef-crest zone (Meselella, 1968; Meselella et al., 1970). As seen in Figure 1, the elevations of these coral assemblages on the terrace surfaces are very similar to the depth-zonation on mid-twentieth century Jamaican reefs (Meselella, 1967). In his analysis of the terraces,

Meselella also observed reefs with two main types of facies sequences: those with over-thickened reef-crest units, and those with a shallowing-up sequence which started in deep head corals and finished in reef-crest or rear-zone facies (Meselella et al., 1970). The first sequence he attributed to a keep-up response to rising SL, and the second to a prograding response to a semi-stable SL. Based on known rates of SL rise, uplift, and reef growth, he speculated that reefs did not initiate on Barbados until later stages of the transgression, when the rise slowed and approximated accretion rates of the reefs (see Meselella et al., 1970, Fig. 16). He postulated that this late transgressive stage of reef development was initially characterized by vertical accretion of facies producing an over-thickened sequence, and then to progradation as relative stillstand conditions prevailed.

The fundamental problem with this keep-up and prograde model was that Meselella was uncertain as to what facies lay at the base of the terraces because shallow road-cuts provided no exposure. He postulated that reef bases may have started either as a pioneering assemblage of deep-water corals that built up into a climax reef-crest community, or initiated with a full zonation that responded directly to SL rise. Furthermore, he acknowledged that his model could not account for certain morphological anomalies in the LIG reef terrace. For example, a reef terrace on the south coast is split into two sub-terraces which are both rimmed by facies containing the reef-crest coral *A. palmata* (Figure 1). Subsequently, Ku et al. (1990) interpreted the lower terrace, informally known as the “Maxwell Hill” sub-terrace, as a reef-crest-lagoon unit and suggested that this division might represent stratigraphic evidence of a double highstand (Figure 1). Upon dating, however, he could not detect any significant age difference between the two sub-terraces. More recently, Schellmann and Radtke (2004) redated these two sub-terraces using electron spin resonance and claimed significant age differences between terraces, with the upper terrace being older (128 ka) than the lower (118 ka).

Unfortunately, there are problems with the analysis of Schellmann and Radtke (2004). First, the terrace ages have analytical errors as large as their age differences, and the age ranges for each terrace overlap to such an extent that the new age designations are effectively meaningless. Second, no facies analysis of the lower sub-terrace was presented to support the claim that it was a reef-crest-lagoon system (as suggested by Ku et al. [1990]). And third, it ignored a detailed facies analysis by Blanchon and Eisenhauer (2001), which confirmed that a true reef-crest facies was absent from the lower Maxwell Hill subterrace (Figure 1). In fact, these new facies data showed that the two sub-terraces combined have a facies zonation that is consistent with a single-reef system, with the upper sub-terrace encompassing the rear zone and a high-energy reef-crest facies, and the lower sub-terrace the reef-front *A. cervicornis* facies and a peripheral ridge of inter-grown thickets of *A. palmata* and *A. cervicornis* (Blanchon and Eisenhauer, 2001). That *A. palmata* is



**Last Interglacial and Reef Development, Figure 1** Stratigraphy and architecture of the uplifted LIG reef terrace around Barbados compared to the same scale with modern-reef architecture from the north coast of Jamaica (ca. 1950). Comparison of coral depth-zonation from the modern reef, with the surface-facies depth-zonation from the reef terrace, shows a concordant depth-zonation. This concordance facilitates a reconstruction of the fossil-reef response to SL rise, and shows that along the south coast of the island, LIG reefs had a vertical or prograding keep-up architecture. Along less-exposed sections on this coast, the reef developed two sub-terraces and a sill reef. Note also an intertidal notch at ~3 m above terrace surface at Gibbons. Along the west coast of the island, the reef terrace developed a retrograding keep-up architecture. These different variants of keep-up architecture are a response to weaker wave-fields along the protected west coast.

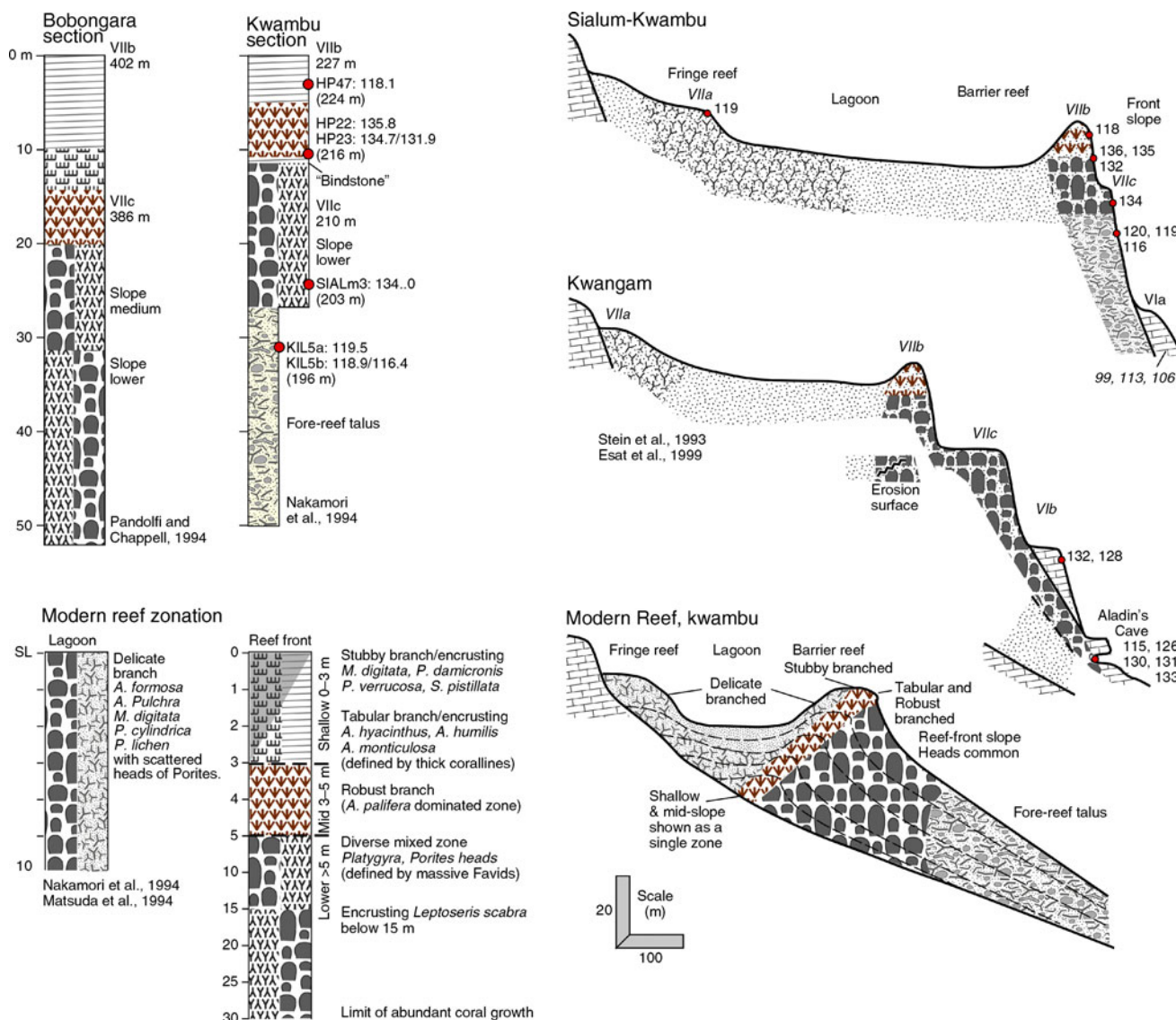
inter-grown with the fragile-branching *A. cervicornis* in these thickets, and that neither are coated with shallow encrusters, indicates that the peripheral ridge was a submerged shelf-edge feature, not a reef-crest. This is also supported by the fact that ridge development is restricted to exposed east-facing sections of the sub-terrace where higher wave-energy would have encouraged deeper *A. palmata* development seaward of the crest. Similar ridges, known as sill- or shelf-edge reefs, are common in the Caribbean and have been reported rimming the north coast of Jamaica, the western shelf of Barbados, the Belize Barrier Reef, and the island of Grand Caymen (Goreau and Goreau, 1973; Rützler and Macintyre, 1982; Macintyre et al., 1991; Blanchon and Jones, 1997).

Apart from resolving morphological complications, Mesolella's keep-up and prograde model has also been reevaluated by Speed and Cheng (2004), who reported an unusually deep road-cut on the west coast that exposed the terrace base (Figure 2). That section showed a thin

basal unit of *A. palmata* clasts, in-place head corals, and *A. cervicornis*, rising 20 m laterally upslope beneath a thick reef-front unit of *A. cervicornis*. The basal unit was interpreted by Speed and Cheng (2004) to be a low-energy fringe reef which kept up with SL rise and produced a retrogressive and diachronous layer that was progressively buried by an *A. cervicornis* facies forming seaward in deeper water. This section therefore provided an answer to Mesolella's dilemma, and proved that reefs did not progress from deep-water pioneer into a shallow climax communities as they caught up with SL, but initiated as fully zoned reefs that responded directly to SL rise, producing a clear keep-up response.

The new retrogressive keep-up model of west-coast terraces was inferred by Speed and Cheng (2004) to exist widely in other Barbadian terraces. But it is unclear how applicable their model is to terraces on the southeast coast, which developed under higher-energy wave-fields and developed more extensive reef-crests with significant





**Last Interglacial and Reef Development, Figure 2** Stratigraphy and architecture of the uplifted LIG reef terrace along the Huon Peninsula compared at the same scale to local modern-reef architecture (strictly reliable ages shown in *bold*). Note that like its modern counterpart, the fossil terrace has an inner-fringe reef and an outer-barrier reef, but they are at different elevations implying that the terrace is tilted and/or has been substantially eroded. The latter process would also account for the narrowness of the fossil barrier reef compared to the modern. Compared to the modern architecture, vertical sections from the LIG terrace show expanded facies depth-zones, with mid- and shallow-slope assemblages being as much as 20 m thick compared to 5 m in modern. This implies that they kept up with rising SL during the penultimate deglaciation. These sections do not represent the entire sequence, however, which is as much as 90 m thick and at least one shallow-water unit has been identified at the base of the reef-front slope (in Aladdin's Cave). This is clearly inconsistent with continuous reef development which should, as seen from the modern architecture, produce a simple shallowing-up facies sequence if the reef had a prograde keep-up architecture.

topographic relief (Figure 1). From this area, for example, Blanchon and Eisenhauer (2001) reported a 17 m thick reef-crest section composed of in-place *A. palmata* colonies and their boulder-sized fragments, topped by a 3 m back-reef unit dominated by diverse branching corals (Figure 1). They interpreted this section to represent a keep-up reef which initially aggraded vertically in response to a SL rise of between 14 and 20 m, and later

underwent progradation to produce a cap of back-reef facies. As a consequence, Mesolella's keep-up and prograde model may better represent terrace architecture along the southeast coast, whereas Speed and Cheng's retrogressive keep-up model better represents west-coast terraces. However, exclusive application of either model to Barbadian reef terraces clearly underestimates the role of wave-energy in shaping reef architecture (Yamano et al., 2003).

Recent refinement in the precision of U-series dating has encouraged several attempts to date the early stages of reef development exposed in these deep sections. Dates from the 17 m thick reef-crest section from the southeast coast reported by Blanchon and Eisenhauer (2001) were affected by diagenesis, and even those with reliable isotopic signatures showed no stratigraphic consistency. In the middle of the unit, a single, strictly reliable age of 129 ka suggested a significant part of the reefs development predated the insolation maximum. But absence of replicate ages from this sample means that true-age variation and hence the samples reliability cannot be verified. A further attempt was made by Gallup et al. (2002), who dated samples from the deep west-coast road-cut using both  $^{230}\text{Th}$  and  $^{231}\text{Pa}$  isotopes. Although these two chronometers have similar chemical affinities and the same uranium parent isotope, they provide an independent check on true-age variation of the sample (Edwards et al., 1997). A single, isotopically pristine coral from the base of the terrace gave concordant ages of 136 ka, indicating that it grew during the penultimate deglaciation at an equivalent depth of 18 m below present SL (Gallup et al., 2002). If this age is accurate, it implies that SL had completed 80% of its rise prior to the insolation maximum, indicating that other factors besides orbital forcing may have been involved in this early deglaciation. Samples from a lower unit also gave concordant ages of 129 ka implying that the SL rise was interrupted by a reversal before attaining its highstand. Subsequent work by Speed and Cheng (2004), however, demonstrated that corals in this lower unit were detrital and thus have no significance for SL. In addition, more precise ages from speleothems indicate that glacial termination II started at 129 ka (Chen et al., 2009), casting doubt on claims of early reef development and the  $^{231}\text{Pa}$  method of age verification.

### Huon Peninsula, Papua New Guinea

The age and elevation of uplifted flights of reef terraces on the Huon Peninsula have also been the subject of extensive study and used to corroborate the SL change and ice-volume over the last glacial cycle (Chappell, 1974, 2002; Aharon and Chappell, 1986; Chappell and Shackleton, 1986; Stein et al., 1993; Esat et al., 1999). Although it is clear that the age of successive terraces increase upslope, and that they consist of shallow-water corals, the fundamental basis of SL reconstructions from individual terraces is their comparison with the depth-zonation and architecture of local modern and Holocene reefs. Unfortunately, little is known about these reefs or their development (Edinger et al., 2001). As summarized in Figure 2, basic descriptions of local reefs have been reported by Chappell (1974) and Nakamori et al. (1994) who indicate that they consist of a fringing and barrier-reef complex separated by a narrow sediment-dominated lagoon. Although not present in the lagoon, a depth-zonation based largely on the presence of coralline algal

crusts and coral morphology has also been reported from the barrier crest down the seaward slope by Nakamori et al. (1994) and Matsuda et al. (1994).

A quantitative analysis of coral assemblages on the crests and slopes of the Pleistocene terraces found that, although zonation of assemblages generally reflected the modern zonation, it could only be reliably differentiated using the presence or absence of thick crusts of coralline algae (Pandolfi, 1996). In most sections, coral communities shared more than half of their common species, and in places zonation was almost indistinguishable. The only indicator was the greater occurrence of *Fungia* spp. and Favid head corals in the lower-slope zones. Additional differences between the modern and fossil communities was that fragile-branching corals were underrepresented in slope sections and some exclusively upper-slope corals on modern reefs, such as *A. gemmifera*, were also common in the deep slope assemblage of the fossil reefs, indicating down-slope transport (cf. Van Woesik et al., 1991).

For the LIG terrace in particular, measured sections at several locations show that reefal zonation is similar to the Holocene, consisting of a fringing reef, a lagoon, and a barrier-reef complex (Chappell, 1974; Aharon and Chappell, 1986; Pandolfi and Chappell, 1994). But these sections also show that individual reef zones are much thicker than in the modern-reef zonation, indicating that the LIG reef complex likely responded to rising SL (Figure 2). A similar response was identified from the Holocene reef complex itself, where a 52 m over-thickened reef unit was recovered from a bore-hole on the barrier crest (Chappell and Polach, 1991). Dating of corals in this core showed that reef development initiated 13 ka ago but ceased by 6 ka due to uplift (Chappell and Polach, 1991; Edwards et al., 1993; Ota and Chappell, 1999). On the basis of these data, several workers have proposed that reef development during the LIG and Holocene had a simple progradational architecture with the barrier crest keeping pace with SL rise and migrating over its seaward slope (Chappell, 1974, 1980; Chappell and Veeh, 1978; Chappell and Polach, 1991; Ota and Chappell, 1999). Yet this keep-up model is not adequately supported by the data, given that neither coral zonation nor facies geometries have been fully established for either the LIG or Holocene reef complexes. It could be, for example, that reefs did not always maintain their position at SL, and may have been outpaced by meltwater pulses.

In fact, investigation of the LIG terrace has found that a simple keep-up reef architecture is difficult to reconcile with the actual stratigraphy, which apparently shows significant complexity (Stein et al., 1993; Esat et al., 1999). For example, between the Kwangam Gorge and the slopes above the villages of Sialum and Kwambu, there are several well-studied sections through the fringing, lagoon, and barrier-reef complex (Figure 2). These sections show that the outer barrier (terrace VIIb) forms a narrow ridge with local reef-crest remnants (Stein et al., 1993). Its seaward face exposes coral and *Halimeda* gravels with

patches of deep-water coral further down-slope. Behind the barrier, the lagoon is dominated by skeletal sand interspersed by patch reefs, and passes laterally into coral thickets of the fringing reef (terrace VIIa). This double-reef complex is dissected by the Kwangam Gorge, where the fringing reef is seen to pass beneath the lagoon floor into the barrier (Bloom et al., 1974). The gorge also exposes an erosion surface ~20 m below the barrier crest sloping gently for some 30 m into the lagoon, but it shows no evidence of subaerial exposure (Stein et al., 1993). Although laterally discontinuous, this erosion surface was interpreted as separating the two reef units and indicating that the barrier reef disconformably overlies the fringing-reef unit (Chappell and Veeh, 1978). Part of this interpretation was clearly based on different alpha spectrometric U-series ages that were reported early on from the two reef-crests by Veeh and Chappell (1970) and Bloom et al. (1974). But recent dating using more precise and better screened U-series ages has failed to replicate these early results, and has also identified significant age inversions down the barrier-reef slope where no evidence of stratigraphic discontinuity exists (Stein et al., 1993).

A similar erosion surface was observed to divide reef units in the Sazum River gorge, a further 10 km to the northwest (Aharon et al., 1980; Aharon and Chappell, 1986). At this location, a 30 m barrier-reef section erosively overlies a 70 m thick reefal unit that was implicitly assumed to be a seaward extension of the fringing-reef unit (Figure 2). However, this underlying reefal unit was also encountered in "Aladdin's Cave" located some 90 m below the barrier crest close to the Kwangam gorge (Esat et al., 1999). A shallow head-coral assemblage found in the walls and floor of the cave imply that this underlying reef unit is an early transgressive reef that accreted vertically in response to the deglacial SL rise, as has also been illustrated for the Holocene reef terrace (Chappell and Polach, 1991; Ota and Chappell, 1999). Corals from this cave returned seven isotopically acceptable  $^{230}\text{Th}$  ages of between 125.6 and 133.7 ka (i.e., a 7.2 ka true-age variation). These were averaged by Esat et al. (1999) to assign an age of 130 ka to the cave reef (ignoring a reliable age of 115 ka), and then compared to an average of 134 ka assigned to the barrier crest from four corals dated by Stein et al. (1993), (again ignoring four significantly younger ages also reported by those authors). By comparing the average age and elevation of these two coral groups, Esat et al. (1999) claimed that SL fell rapidly, at least 70 m from the 134 ka barrier-crest group to the cave group, and then rose rapidly, at least 85 m from the 130 ka cave group, with both the fall and the rise occurring within the 4 ka difference between groups. Unfortunately, the validity of this comparison is questionable given that it ignores younger ages from the cave site as well as those from the barrier-crest site reported by Stein et al. (1993). It is much more likely that these stratigraphic age inversions reflect true-age variability (Scholz and Mangini, 2007) and that the cave is simply the oldest part of terrace VII which accreted vertically as SL rose.

It is clear from the foregoing, that the interpretation of LIG reef architecture in the Huon Peninsula has been obfuscated by various attempts to obtain a terrace chronology. The fundamental problem has been that unreliable U-series age determinations, which clearly fail any test of stratigraphic consistency, have driven the analysis of the stratigraphy itself, rather than the other way round. This has led to disconformities being inferred between stratigraphically inverted ages, or inverted ages simply being ignored, rather than acknowledging that many dates have large true-age variabilities and that more than 50% of those with "reliable" isotopic signatures have discordant  $^{231}\text{Pa}$  ages (Scholz and Mangini, 2007). As a result, SL histories determined from these inadequate data are premature, especially interpretations of extreme excursions based on ages alone (Esat et al., 1999).

Furthermore, and as noted by Pandolfi and Chappell (1994, p. 138), widely spaced stratigraphic sections are merely "one-dimensional sloping profiles of three-dimensional reef structures" and say little about stratigraphic architecture, which has been poorly documented in the area. And what little stratigraphic detail has emerged has been over-interpreted. Erosion surfaces which lack evidence of subaerial exposure are clearly difficult to interpret in the absence of supportive contextual data, given that they can be produced by processes other than SL fall. Likewise, it is premature to apply a keep-up model of interglacial reef development in the absence of internal facies geometries from either the LIG or Holocene terraces. Even the Holocene reef structure, which has been described from a long bore-hole (Chappell and Polach, 1991), lacks a taxonomy to species level and thus identification of coral zonation (biofacies) data, making interpretation of SL history or reef response difficult to substantiate (cf. Chappell and Polach, 1976).

## Red Sea

The Red Sea is an active continental rift system related to the development of a spreading center between the African and Arabian plate. Dynamic interplay between rift tectonics, halokinetic faulting, volcanism, climate, and SL variation during the Quaternary has produced a complex stratigraphy where abrupt facies changes between river alluvium, alluvial fans, reef, lagoon, Salina, and beach units, make it difficult to correlate between areas and unequivocally separate tectonic from eustatic SL events (Plaziat et al., 1995). This complexity, together with incomplete exposure and limited uplift of LIG deposits, makes it a difficult area to investigate either interglacial duration or highstand character. Nevertheless, several investigations of reef development during the LIG have been reported from the Egyptian and Eritrean coasts of the Red Sea.

Along the coast of Eritrea, an uplifted and tilted LIG reef sequence near Abdur shows two main stages of shallow-reef development (Walter et al., 2000; Bruggemann et al., 2004). The lower unit is composed of fringing-reef



tract with extensive sandy lagoonal and scattered patch reefs. The reef-crest facies consists of dense thickets of *Goniopora* sp. and *Stylophora pistillata* and forms a shallowing-up sequence, indicating seaward progradation. The lower unit is truncated by an intermittent marine-erosion surface that shows evidence of being both bioeroded and burrowed suggesting that in some areas the surface was a firm ground and not completely cemented. This surface is directly overlain by a second but more limited fringing-reef tract consisting predominantly of reef-crest and reef-front units with a diverse assemblage of in-place corals (Bruggemann et al., 2004).

These two superimposed reef tracts therefore have a back-stepping architecture, which implies that the first stage of reef development was abruptly terminated and was followed by the relocation and reinitiation of the second reef-crest further inland over the former lagoon. Bruggemann et al. (2004) interpreted this reef demise and relocation to have resulted from a brief eustatic SL fall, but could not find any evidence of subaerial exposure associated with the marine-erosion surface. The discontinuous nature of the erosion surface, and the fact that the surface was not completely cemented, is inconsistent with SL fall, and in fact suggests the opposite scenario whereby reef back-stepping may have been the result of a rapid rise of relative SL. Whatever the interpretation, however, the neotectonic setting of the site means that the possibility that coseismic displacement was the cause of reef back-stepping cannot be discounted.

Along the Egyptian coast, in the northern Red Sea, two episodes of deposition during the LIG have been described by Plaziat and others (Plaziat et al., 1998a, b; Orszag-Sperber et al., 2001). During the first stage, fringing-reef tracts topped by beach gravels developed along the coast at elevations between +5 and 10 m. This stage was followed by a down-cutting erosive event that excavated small basins behind breaks in the reef crest. The first depositional event in these depressions was a thin sequence of open-marine sediments containing molluscs and in-place corals. This was followed by a thicker sequence of laminated subaqueous gypsum topped by tepees that reached an elevation of ~3 m below the reef-crest. The final filling unit consisted of massive gypsum consistent with an emergent sabkha environment.

This unusual sedimentary sequence was interpreted to result from a rapid SL fall of ~10 m which caused the excavation of the back-reef depressions (Orszag-Sperber et al., 2001). The subsequent rise of SL back to the same level as before (within 1–3 m) led to the filling of the depressions. The abrupt transition from an open marine to restricted deposits in this fill-sequence was postulated to result from a brief pluvial episode that increased input of sediment to the coast and occluded the gap in the fringing-reef unit, thus sealing the depressions off from the marine environment (Plaziat et al., 1998a; Orszag-Sperber et al., 2001). However, other interpretations are also consistent with these stratigraphic data. For example, down-cutting could result from a rapid SL rise and

reworking of back-reef deposits during storms and sediment export through the reef gaps. These open-marine conditions would favor the initial deposition of open-marine faunas and the abrupt change to restricted environments would mark the start of SL fall at the end of the LIG. That no deepening of these depressions occurred during the ensuing glacial fall in SL, lends support to this latter interpretation. However, confirmation of either interpretation requires a precise chronological framework which is still lacking in this region.

### Reef development in more stable terrains

Reef development in stable sites can provide a detailed look into the timing and duration of peak interglacial conditions during the highstand, as well as the absolute elevation and SL behavior during that highstand. Detailed descriptions of LIG reefs in stable areas have traditionally concentrated along the southern passive margin of the North-American Plate, including sites in Florida, the Bahamas, the Caymans, and the Yucatan. But recent work has also been reported along the Western Australian passive margin of the Indo-Australian Plate from Cape Range to Cape Leeuwin. This facilitates a comparison of reef development within each region and between regions themselves.

#### Florida

Pleistocene reef development in Florida's Key Largo Limestone was described as early as the late eighteenth century (Agassiz, 1896), but it was not until the mid-1960s that U-series dating proved that those elevated reef deposits were of LIG age (Broecker and Thurber, 1965; Osmond et al., 1965). As its name suggests, the reefal Key Largo Limestone is best developed along Key Largo and Windley Key where it forms a broad ridge that rises to a level of +3 m (Harrison and Coniglio, 1985). Although widely cited to reach 5.5 m above mean SL, the original description states that it has an average elevation of +1 m "with local prominences which in two places reach a maximum height of 18 ft" (5.5 m) (Hoffmeister and Multer, 1964, p. 355). At the type locality on Windley Key, the reef unit covers an older topographic high at +1 m, and forms a 2 m thick layer of coalesced patch reefs formed of head corals, particularly *Montastrea annularis*, interspersed with thickets of *A. cervicornis* and small branched *Porites* (Stanley, 1966). The matrix is a skeletal sand composed of mostly *Halimeda* and mollusc fragments. The reef unit gradually dips away from this topographic high and, at its northern and southern outcrop limits, is overlain by or grades into the oolitic sands of the Miami Limestone (Multer et al., 2002). These oolitic units have developed shorelines consistent with a +6 m SL highstand at both Key West in the south and Palm Beach in the north (Hoffmeister and Multer, 1968; Perkins, 1977; Multer et al., 2002). The absence of ooids in the reef matrix and the fact that the reef unit underlies these oolitic sand bodies indicates that reef development likely

preceded the oolite shoreline development during the +6 m highstand (Harrison and Coniglio, 1985). Unfortunately, more precise U-series mass spectrometric dating has been unable to confirm the exact stratigraphic relation between the reef and oolite units due to the impact of diagenesis (Fruijtier et al., 2000), and only one age of 128.1 ka with a strictly reliable isotopic signature has been returned from the reef unit (Multer et al., 2002).

In the absence of reliable ages, the interpretation of reef development in the Key Largo Limestone has focused primarily on the paleo-water depth in which the corals grew. The problem was the lack of evidence for coral zonation or the presence of the reef-crest coral *A. palmata* which might confirm a shallow-water origin. As a result, early interpretations suggested water depths exceeded 6 to 12 m (Stanley, 1966). This was later discounted by evidence of +6 m shoreline development in the oolitic sand bodies (Hoffmeister and Multer, 1968; Perkins, 1977; Harrison and Coniglio, 1985; Multer et al., 2002). All later interpretations therefore favored a shallow, protected, patch-reef setting, but differed according to what afforded that protection. Notions of a reef-crest barrier were finally discounted by drilling data which failed to encounter reef-crest corals and indicated that shelf had a gentle and extensive ramp-style slope which dampened wave development (Multer et al., 2002).

However, these later investigators have failed to pose a more important question: if corals grew in shallow water, then what prevented them from reaching the +6 m highstand? Why was reef development largely restricted to elevations below +3 m and why did it not reach the +6 m highstand attained by the oolitic shorelines either side of the reef tract? Tentative evidence suggests that reef development may have been curtailed by shifting sediment associated with enhanced ooid production during the +6 m highstand. But this needs to be confirmed by precise radiometric ages of both reef and oolitic units.

## Bahamas

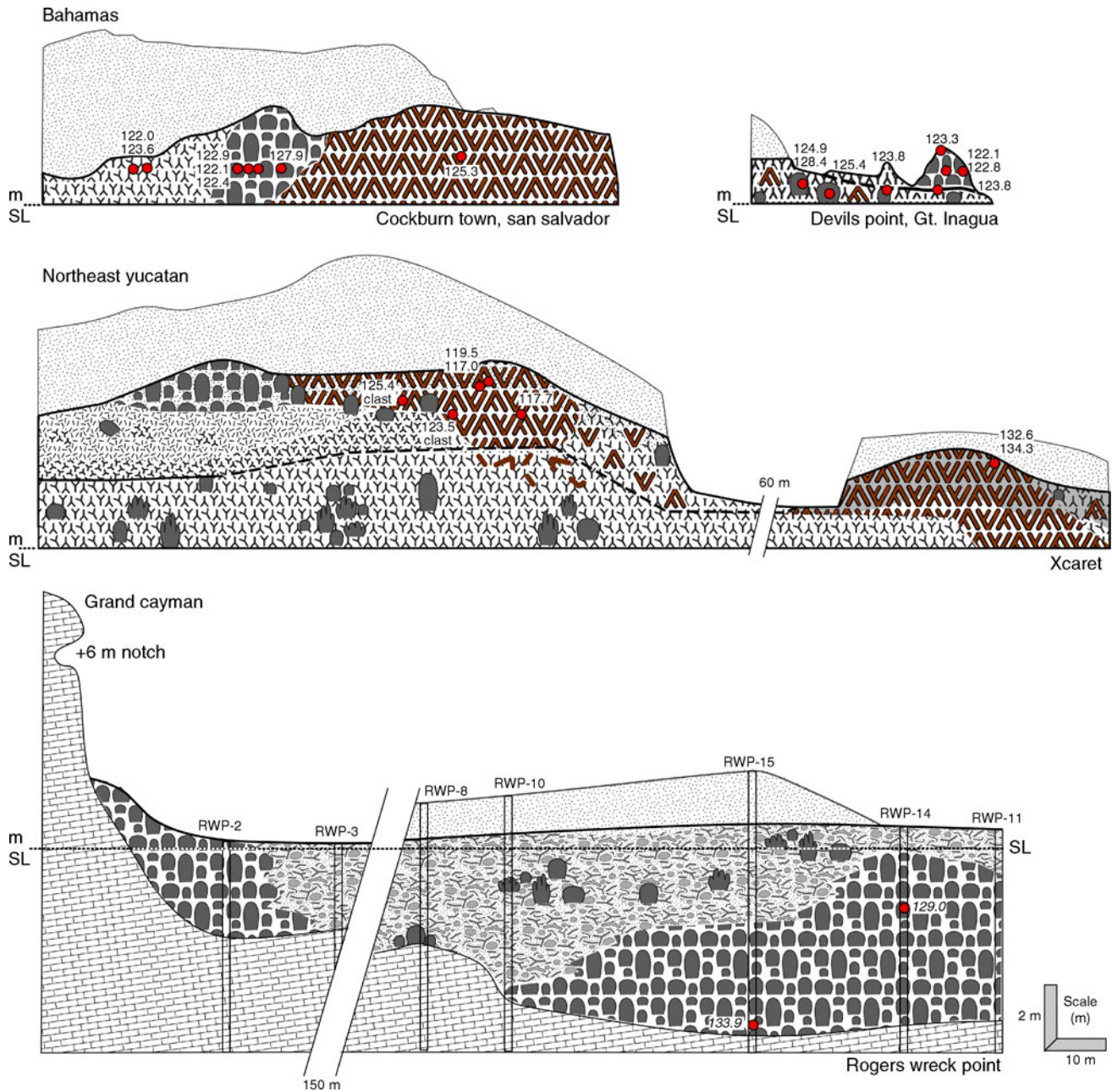
Similar reef development during the LIG has been reported from the adjacent Bahamian archipelago, but it has been characterized best on the island of San Salvador (Curran and White, 1989; Hattin and Warren, 1989; Chen et al., 1991; White et al., 1998; Wilson et al., 1998). There, detailed mapping shows that reefs also reached a maximum elevation of +3 m, and had a simple facies association consisting of a reef-crest, dominated by clasts and colonies of *A. palmata*, flanked by back-reef and a lagoonal zone composed of large patches of *A. cervicornis* and species of *Montastrea* (Figure 3). Above this reefal unit, the marine sequence is dominated by a shallow subtidal and beach-sand lithosome which reaches an elevation of +5 m consistent with a +6 m highstand (Carew and Mylroie, 1997). A similar sequence was reported from the southern end of the island by Hattin and Warren (1989), who documented patch reefs up to +3 m that were topped by a 30 cm cap of the

branching coralline algae. Subsequent development of a separate but poorly developed patch reef above the coralline cap up to 3.5 m was taken to be evidence "...of a slight additional rise of sea level. ..." (Hattin and Warren, 1989, p. 26). From this evidence, they concluded that there was a widespread phase of reef development associated with a +3 m stillstand of SL, followed by a rise to +6 m that was associated with a higher-energy beach and shallow subtidal sequence.

On both San Salvador and Great Inagua further south, systematic dating of the +3 m LIG reef unit revealed that this simple facies association had a rather complex age structure (Chen et al., 1991). Of the 11 samples with strictly reliable isotopic signatures, those taken from in-place corals in the patch reefs were stratigraphically consistent and clustered around 122 ka. But ages from the underlying coral-gravel unit gave a wider range of 122–130 ka, with five ages in excess of 127 ka (Figure 3). Closely juxtaposed samples from that unit also showed large variability of ~5,000 years between corals separated by only a few centimeters (e.g., samples M1, A, and D in Fig. 3a of Chen et al., 1991, p. 88). Although Chen et al. (1991, p. 83) warned that "storms can mix as rubble corals of different ages," well-dated 3 m sections of Holocene and late-glacial reefs show variability no larger than 1,000 years (Blanchon et al., 2002; Edinger et al., 2007). As a consequence, it is unlikely that large magnitude age variability in closely spaced corals from the Bahamian reefs resulted from mixing during hurricanes, as claimed by Chen et al. (1991), but resulted instead from mobilization of U and Th isotopes during diagenesis (Scholz and Mangini, 2007). Coral ages from this unit are therefore unreliable for determining the onset of the sea-level highstand, and cast doubt on the extended duration of the interglacial highstand claimed by Chen et al. (1991).

In addition to the duration of the LIG, these dates have also been used to identify the timing and significance of an internal reef-erosion surface discovered on Great Inagua (White et al., 1998; Wilson et al., 1998). A 1,500-year age difference between coral ages recovered from either side of this surface was taken to indicate that the highstand reef sequence was interrupted by a brief SL fall from +4 m to below the modern datum, and then a rapid rise back to +6 m (White et al., 1998; Wilson et al., 1998). Unfortunately, the 2 ka analytical age uncertainty and large true-age variation in corals dated by Chen et al. (1991) precludes their use in determining the timing of events of such short duration. Furthermore, although there is extensive evidence of marine truncation and bioerosion of corals and their clasts under this surface, there is no reliable evidence of emergence that can be separated from emergence that occurred at the end of the highstand. As a consequence, the evidence for a SL fall is based entirely on marine-erosion which is a common process not specific to that cause.

The +3 m reef unit has also been identified on several other Bahamian islands (Neumann and Hearty, 1996; Hearty and Neumann, 2001). On most of these, reef



**Last Interglacial and Reef Development, Figure 3** Stratigraphy and architecture of the LIG reef terrace from stable sites along the southern passive margin of the North-American Plate. Reef development to +3 m is widespread, but above this elevation reefs are absent in all areas except the Yucatan. Reef absence above +3 m in these areas is replaced by other evidence of a +6 m highstand, such as intertidal notches and sediments. In other words, all sequences support a highstand during the LIG of +6 m but, in most areas, reef development ceased by the time SL reached +3 m. Back-stepping in reef sequence from the Yucatan implies this absence was caused by a SL jump from +3 to +6 m. In most areas, the jump rapidly inundated broad coastal tracts, enhancing sediment flux and altering transport pathways, and this led to widespread reef demise. Reefs only survived in limited areas that were naturally protected from the new sedimentation regime.

development is vertically restricted to less than +3 m. As on San Salvador, however, intertidal beach units and notches clearly indicate that the highstand reached +6 m. Neumann and Hearty (1996) claimed that the general absence of reefal units above +3 m indicated that there

must have been a rapid jump in SL toward the end of the highstand with a duration that was too short for reefs to keep up or even to catch up. In fact, they claimed that there was only sufficient time for notch cutting, which was estimated at 600 years. To account for the well-preserved



nature of the reef surfaces, they argued that the fall from the brief highstand must have been as rapid as the preceding rise, and that the reefs therefore had little time for modification in the marine environment. The brief duration of the +6 m highstand was contested by Carew (1997), who suggested that a slower rate for notch erosion was more representative and gave a duration of 3,000 years as a better estimate. He also questioned the significance of reef preservation indicating that the well-preserved reefs were more likely to have been rapidly entombed by mobile subtidal sand bodies before SL regression.

### Grand Cayman

An almost identical sequence of reef development has been reported from Grand Cayman (Jones and Hunter, 1990; Hunter and Jones, 1996; Coyne et al., 2007), where a lower lagoonal patch-reef unit developed over a wide area but never exceeded an elevation of +3 m (Jones and Hunter [1990] reported patch reefs up to 3.8 m, but these were later corrected to 2.8 m in Jones [1994, p. 32] and Coyne et al. [2007, p. 550]). The patch reefs in this unit were protected to the northwest by a reef tract, also with a +3 m elevation. In most areas, the lower patch-reef unit is overlain by cross-bedded oolitic sands that develop up to an elevation of +6 m. The base of cross-bedded unit is marked by a discontinuous marine-erosion surface which is consistent with an abrupt switch to a high-energy subtidal to intertidal setting. Although Jones and Hunter (1990) interpreted this sequence to represent a simple shallowing-up succession, they omitted to explain why reef development was restricted to +3 m. They also suggested that the erosion surface represented scour during storms, but did not explain why storm waves and shifting sands were suddenly able to invade large areas of an extensive and apparently well-protected lagoon where patch reefs with delicate branching corals had previously flourished.

Later Coyne et al. (2007) suggested that cross-bedded units were younger based on  $^{230}\text{Th}$  ages of marine gastropods. Unfortunately, these ages failed any reasonable measure of isotopic reliability due to open-system diagenesis and were given priority over basic stratigraphic relations, which showed conformable transitions between the patch reef and cross-bedded units in several areas (including newly reported cores from George Town Harbor). As a result, the claim that these units are significantly younger is unsupported by reliable data.

Along the northeast coast of Grand Cayman, Vèzina et al. (1999) also reported a +3 m patch-reef sequence of LIG age adjacent to a relict sea-cliff with a notch at +6 m (Figure 3). Using closely spaced cores, they demonstrated that reef development overlapped the cliff base and reached an elevation of +2.6 m. In the outer part of the section, patch reefs aggraded vertically and then prograded horizontally seaward, as if constrained by a stillstand of sea level (Vèzina et al., 1999). The lack of reef development or any sediment above +3 m was interpreted as

being due to submergence in a lagoonal setting with a +6 m SL. However, in the absence of a preserved reef-crest unit (due to modern coastal erosion) this interpretation is equivocal and ignores the progradation of patch reefs and the fact that, in modern lagoons, patch reefs commonly reach mean low water.

From the foregoing, it is clear that reef sequences in Florida, the Bahamas and the Caymans flourished up to an elevation of +3 m but no higher. The fundamental question is why were reefs restricted to this elevation when there is abundant evidence that SL peaked at +6 m? The claim of Neumann and Hearty (1996) that sea level jumped to +6 m is a possible explanation, but falls short in accounting for why reefs did not recover. Even if the rise was transient, and lasted 600 years as claimed, reefs could have accreted 6 m in that time assuming a conservative accretion rate of 10 mm/years. Clearly something happened during the rise from +3 to +6 m that inhibited reef development in these areas.

### Northeast Yucatan Peninsula

A possible answer to this problem has recently been provided by Blanchon et al. (2009), who reported two superimposed fossil reef-crest units from the northeast Yucatan, one at +3 m and the other at +6 m (Figure 3). Reliable radiometric ages confirmed that both crests were of LIG age, between 125 and 117 ka, but could not differentiate between them due to subtle diagenetic alteration of corals in the lower unit. The relative-age of the two units, however, could be determined from their facies differences and contact relationships. The lower-reef tract at +3 m consisted of an *A. palmata* crest flanked by an *A. cervicornis*-dominated reef-front and a large lagoonal patch-reef complex that extended 200 m inland. Framework in the lower-tract had a cap of coralline algae and, in places, was leveled by a discontinuous marine-erosion surface. The upper-reef tract at +6 m initiated atop the seaward edge of the lagoonal patch-reef complex. But in this new location reef development was significantly different. In the lagoon, frameworks were dominated by a sediment-tolerant assemblage of branching coralline algae and *Porites*. They also lacked a cap of corallines, and were instead infiltrated by beach-derived shell-gravels from regressive shoreface deposits above. This infiltration pattern shows that the upper reef must be younger and was active shortly before SL fell from its highstand.

The cap of corallines on the older +3 m crest attests to its rapid demise and the discontinuous marine-erosion surface indicates that a patchy demise of corals also took place in the lagoon. Importantly, however, areas of continuous accretion between the lower patch-reef complex and the overlying tract require that lower-reef demise was ecologically synchronous with upper-reef initiation. Furthermore, in the upper tract, reef-flat development above +5 m and large in-place colonies of *A. palmata* at the base of the upper-crest unit indicated that SL must have jumped from +3 m to more than +5 m to drown the lower reef and

accommodate the back-stepping of the upper reef (Blanchon, in press). This jump also created a higher-energy wave field that mobilized back-reef and lagoonal sediments, creating a high sediment flux which smothered and eroded lagoonal framework, prevented the recovery of the submerged reef-crest, and suppressed coral framework in the lagoon (Blanchon et al., 2009).

A jump in SL, that caused reef drowning and back-steeping in the Yucatan reef sequence, can also account for the lack of reef development above +3 m in low-lying areas like the Bahamas and Grand Cayman. This is because the SL rise rate during the jump was sufficient to outpace the reef-accretion rate, and submerged +3 m reef tracts everywhere. This rapid depth change induced a higher-energy wave field that not only remobilized lagoonal sediments and buried or eroded adjacent reef framework, but led to a switch in sediment regime by suddenly providing extensive shallow-water areas for the generation of marine sand bodies. This increase in sediment flux prevented many of the submerged reefs from recovering after the rise, and led to a widespread suppression new reef development in low-lying areas. Along narrower, steeper shelves with smaller sediment reservoirs, a lower sediment flux after the jump enabled reefs to recover and back-step to new upslope positions.

### Western Australia

Reef-terrace development at +3 m not only occurs in stable areas of the Caribbean, but has been widely reported along the coast of Western Australia. In a review of Plio-Pleistocene deposits, Kendrick et al. (1991) reported intermittent development of a coral-reef terrace for 2,000 km along this coast, from Cape Range in the north to Cape Leeuwin in the south. Such extensive reef development provides an ideal opportunity to identify the controlling factors on reef development, such as the rate and magnitude of sea-level rise, and to compare those factors with other LIG reef provinces, such as the Caribbean.

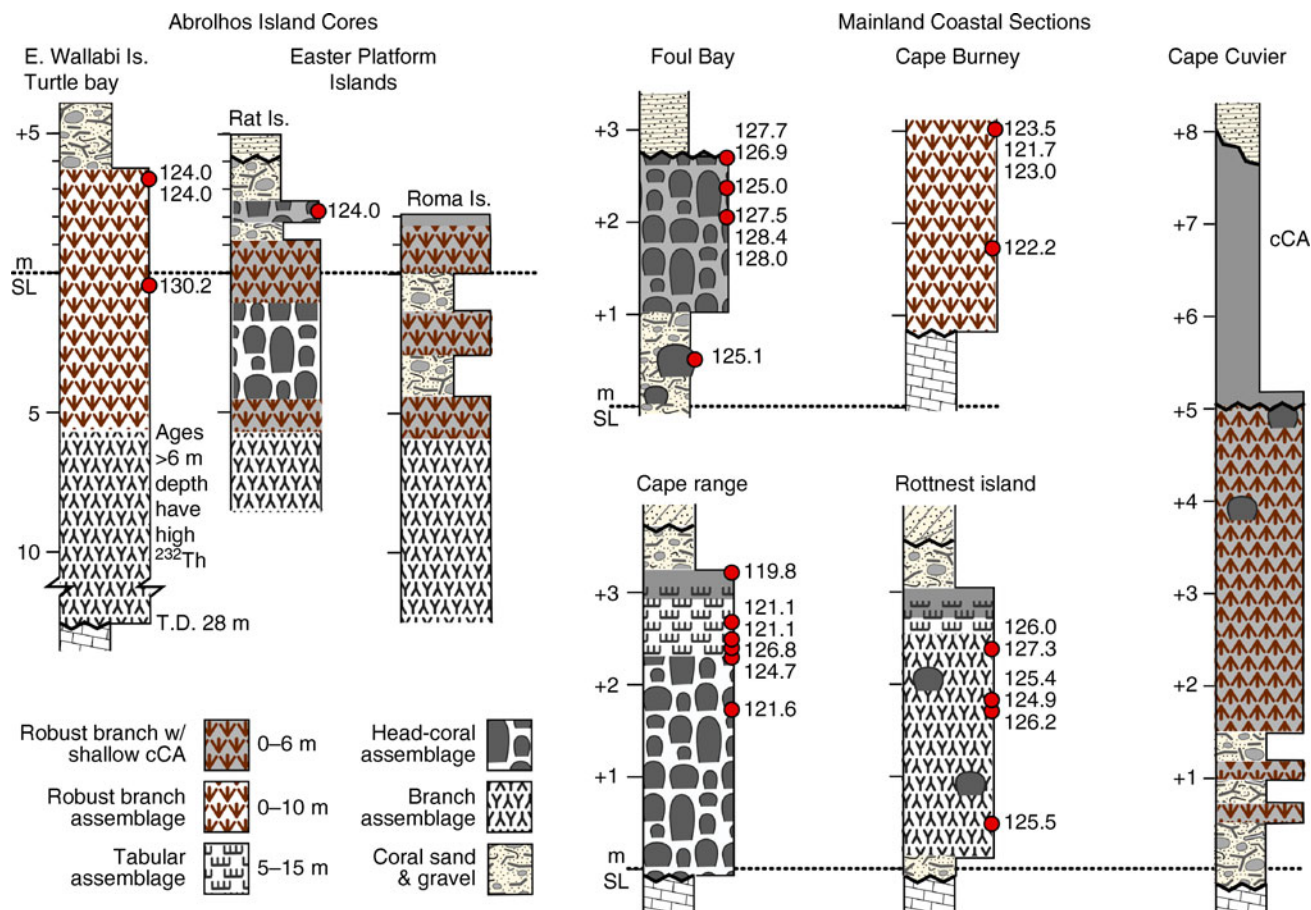
The most northerly report of LIG reef development occurs at Cape Range, in the Canarvan Basin, where a fringing-reef forms a narrow coastal terrace running alongside the modern Ningaloo reef. In some areas, the terrace extends inland and consists of small patch reefs and lagoonal sands and gravels (Kendrick et al., 1991). Several sections in this area were investigated by Stirling et al. (1998), who reported the  $^{230}\text{Th}$  age of reef framework in the narrow coastal terrace at +3 m. Two of those locations yielded several strictly reliable ages: interior lagoonal patch reefs at +2 m in Mangrove Bay, gave ages from 116.1 to 119.2 ka, whereas a +3 m coastal reef tract further south at Yardie Creek gave four ages between 119.8 and 121.6 ka with two outliers of 124.6 and 126.8 ka (Figure 4). Drilling on the +2 m terrace at Tantabiddi Bay, just north of Mangrove Bay, recovered framework as deep as 10.3 m below SL, but no characterization of the core was provided (Stirling et al., 1998).

Further inland, along the sheltered coast of the Sandalwood Peninsula, Greenstein et al. (2005) discovered a marine-erosion surface truncating a +1.5 m reef terrace. Some areas of this surface were recolonized by sparse coral heads, but evidence of subaerial exposure was absent, making it identical to other marine-erosion surfaces reported from LIG reef deposits elsewhere.

At Cape Cuvier a little further south, O'Leary et al. (2008a) reported fringing-reef development in a coastal terrace that sloped inshore from +3 to +5 m. Like the terrace to the north, corals on the surface were truncated and capped with a layer of coralline algae. But unlike elsewhere, this coralline cap extended further upslope to +8 m, where it covered the inclined wave-cut surface of the underlying tertiary eolianite (Figure 4). Above that elevation was a coral-cobble beach gravel. Unfortunately, all  $^{230}\text{Th}$  ages measured from corals in this exposure had isotopic signatures associated with open-system diagenesis, but they clearly indicate a LIG age for the deposit. At Shark Bay, 200 km further south, O'Leary et al. (2008b) also documented reef development in a horizontal coastal terrace at +2.5 m. This terrace yielded isotopically reliable but stratigraphically inconsistent ages between 125.4 and 128.8 ka.

Continuing south into the Perth Basin, several sites have been investigated around Geraldton, including Burney and Leander Points on the mainland, and particularly the Houtmann Abrolhos Islands some 60 km offshore (Figure 4). In the Abrolhos, the reef terrace normally reaches +2 to 3 m and, as in other places, is thinly capped by crustose corallines. This reef framework is then overlain by up to 2 m of skeletal sands and gravels deposited in shallow subtidal or intertidal conditions. An exception to this sequence is found on east Wallabi Island at Turtle Bay, where the top of a domal exposure of reef framework reached +4 m and lacked the normal cap of coralline algae (Zhu et al., 1993). Subsequent drilling and dating of the Turtle Bay unit by Eisenhauer et al. (1996) gave two reliable surface ages of 124.0 ka and an outlier at 130.2 ka, and recovered 32 m of branching-coral framework. Drilling was also performed on the +2 m terrace at Rat and Roma Islands in the Easter Group of the Abrolhos by Collins et al. (1993). Both sequences were again dominated by branching corals but showed abundant encrustation by corallines. Only one reliable age of 124.0 ka was recorded from the surface exposure on Rat Island.

More successful dating of the +2 to 3 m reef terrace has been made on the adjacent mainland sections at Burney and Leander Points (Stirling et al., 1995, 1998). Interestingly, both these sections recorded multiple reliable ages that were similar to the Abrolhos. At Leander point, corals from a 1.5 m interval just above sea level recorded six ages from 121.8 to 124.2 ka with a single outlier of 126.6 ka. Similarly at Burney Point, four corals from a 1.3 m interval at the top of the terrace recorded ages between 121.7 and 123.5 ka. Clearly, these data convincingly demonstrate that coastal reef terrace in this region had a restricted interval of development between 124 and 122 ka.



**Last Interglacial and Reef Development, Figure 4** Cores and coastal sections from the LIG reef terrace from sites along the stable western Australian passive margin of the Indo-Australian Plate. Like other passive-margin sites, reef development to +3 m is widespread but, above this elevation, reefs are absent in all areas except Cape Cuvier (which is consequently thought to be a site of local uplift). Other evidence of a +6 m highstand, such as sub- and intertidal sediments, has been documented in most of these areas. This again suggests that all sequences support a highstand during the LIG of +6 m but, in most areas, reef development ceased by the time SL reached +3 m. As yet, back-stepping reef units have not been found in this region. When corrected for stratigraphic consistency, strictly reliable ages from several sections show that this +3 m reef development occurred within a restricted interval from 124 to 120 ka ago.

The reef terrace at Burney Point was also described in some detail by Johnson et al. (1995), who documented a wave-sculptured disconformity surface at +1 m overlain by a collapsed thicket of robust-branching *Acropora* that reached an elevation of +3 m (Figure 4). The disconformity preserved beneath the reef unit at this site has been used as an analog for the erosion surface described from Devils Point, Great Inagua, in the Bahamas (Wilson et al. 1998). Although the surfaces are similar, in that they are both bioeroded and encrusted, the surface at Burney Point has been highly sculptured by wave-erosion producing a widespread ridge-and-runnel system with a relief of 30 cm. Neither the erosion surface from the Bahamas, nor those in any other LIG reef sequence described so far, have this kind of wave sculpturing, which should be present if they had experienced a double passage of the intertidal shoreface during a meter-scale negative SL excursion.

The LIG reefs in the Abrolhos Islands and near Geraldton coincide with the present limit of modern-reef development. But unlike the modern reefs, LIG reef development continues south, and the +3 m reef terrace has been reported a further 350 km south at Rottneest Island, as well as in Foul Bay near Cape Leeuwin, some 550 km south of the modern-reef limit. Reef development at Rottneest Island is briefly described by Playford (1988) and dated by Stirling et al. (1995). At Salmon Bay, on the south coast of the Island, a coastal exposure of reef framework dominated by branching and tabular *Acropora* species reaches +3 m (Figure 4). Corals from this exposure returned five ages between 124.9 and 126.2 ka and an outlier of 127.3 ka. At Foul Bay, McCulloch and Mortimer (2008) reported a 1 m thick reef unit that reached +2.8 m which consisted of toppled and in-place head corals and coralline algae. Corals in this 1 m thick



unit returned isotopically reliable ages from 125.0 to 128.4 which is a significant age range considering the limited thickness of the unit. This lack of stratigraphic consistency indicates these ages may be suspect.

The expansion of sub-tropical reefs some 550 km past the modern limit of reef development, clearly indicates warmer sea temperatures than present during the LIG (Kendrick et al., 1991). This expansion was examined in detail by Greenstein and Pandolfi (2008), who contrasted modern and Pleistocene coral-assemblage pairs from Cape Range to Rottnest Island, a latitudinal gradient of 12°. They found that in the north, between Cape Range and Abrolhos, modern and fossil reefs had similar assemblages. But for sites further south, from Geraldton to Rottnest, coral taxa were different and fossil reefs were dominated by acroporas (*A. palifera*, *A. humilis*, and *A. hyacinthus*). In other words LIG reefs at Rottnest Island had a coral assemblage equivalent to the northern modern reefs, rather than the present assemblage around the island. This could be a preservational bias due to erosion of the fossil reefs, but of the 31 fossil taxa, 8 had significantly expanded ranges. In addition, corals such as *A. palifera*, which today is only found north of Cape Range, occurred south of the Abrolhos during the LIG. These results are clearly consistent with a shift in the biogeographic boundary of reef development and also a reduced latitudinal temperature gradient during the LIG.

In terms of timing of the biogeographic shift, Greenstein and Pandolfi (2008) assumed that the range expansions of coral taxa were contemporaneous and that reef-building events occurred during the same time interval. However, an analysis of the geochronology of reef development at the same sites by McCulloch and Mortimer (2008) concluded that the expansion of these taxa may have been confined to the early part of the LIG between 129 and 125 ka. Such claims are clearly hinged on the reliability of the  $^{230}\text{Th}$  ages and, given that there has been little assessment of the true-age variation in corals at these sites it is difficult to rule out the possibility that apparent age differences between the LIG reefs of Western Australia are merely dating artifacts due to subtle diagenetic processes, perhaps related to the increasing aridity to the north.

From the foregoing, it is abundantly clear that there was widespread reef development along the coast of Western Australia during the LIG. Of the 16 sites described above, 12 have a reef terrace at or below +3 m which is consistent with an initial +3 m SL position. Of the remaining four sites, three have reef terraces between +3 and +4 m. And the final site, at Cape Cuvier, shows evidence for two sea-level positions, with a reef terrace at +5 m and a coralline-encrusted shore platform up to +8 m. Although it has been claimed that the Cape Cuvier site represents evidence of a highstand greater than +6 m (O'Leary et al., 2008a), it is evident that the elevation of the reef and shore platform is anomalous in comparison with all other sites. This in itself is significant evidence for neotectonic activity, but is also supported

by the site's location on the western flank of the Cuvier Dome (Logan, 1987). Interestingly, if we assume that the reef terrace was uplifted from an original elevation of +3 m, then this implies that sea level must have subsequently risen to highstand of +6 m at the end of the LIG – a conclusion that is supported by elevations of SL indicators from other parts of Australia (Murray-Wallace, 2002).

Stratigraphic analysis of the radiometric ages of corals in the +3 m reef terrace indicates that widespread reef development along the Western Australian coast was confined to a much narrower time window than implied by the simple spread of ages alone (Table 1). Clearly, the amount of time represented by a 3 m interval of conformable reef framework depends directly on the rate of reef accretion and the precision of the age determination. During the last deglaciation, for example, reefs accreted at rates of up to 3 m in 375 years during the rapid postglacial SL rise (Blanchon, this volume). Measurement of the extrinsic age variation in uplifted Holocene reefs on the Huon Peninsula shows that a 3 m stratigraphic interval took no more than 1,000 years to develop (Edinger et al., 2007). Assuming the conservative estimate and an analytical error of 1,000 years, this indicates that the age of +3 m reef terrace along coastal areas of Western Australia should vary by no more than 1,000 years,  $\pm 1,000$  years (Blanchon et al., 2009). As shown in Table 1, Yardie Creek in the north, Burney and Leander Points in the centre, and Rottnest Island in the south all have strictly reliable age ranges of <2 ka and are therefore stratigraphically consistent. The mean ages from these sites indicates a restricted age of reef development between 120 and 124 ka for all but Rottnest Island where the average age is 126 ka.

## Hawaii

In addition to areas that have been largely stable since the LIG, there are some areas that have undergone minor amounts of gradual uplift thereby better exposing reef development. For example, adjacent to the island of Hawaii, where active volcanic loading has depressed the lithosphere, lies the smaller island of Oahu. This island sits upon the peripheral bulge of the loaded crust and, in contrast to the bigger island, has undergone slow uplift which has preserved and elevated LIG deposits up to +13 m (Muhs et al., 2002). These deposits consist of in-place reef framework, overlain by erosively-based intertidal skeletal sand and gravel units, but very few have been reported in any stratigraphic detail (Stearns, 1974; Ku et al., 1974; Sherman et al., 1993; Szabo et al., 1994). Recently Muhs et al. (2002) reported an extensive data set of 37 high-precision  $^{230}\text{Th}$  ages from this island and claimed that the duration of the LIG extended from 136 to 115 ka and therefore predated the insolation peak as claimed by Szabo et al. (1994) on the basis of less precise ages. However, there are significant problems with this analysis. First, Muhs et al. (2002) considered all ages with initial ratios of  $149 \pm 8$  per mil as reliable, rather than

**Last Interglacial and Reef Development, Table 1** Summary of age, elevation, and character of coastal reef terrace, Western Australia

| Area/site/reference              | Elevation (m) | SR age (ka) | SC age range (ka) | Coral assemblage                                                                                                 |
|----------------------------------|---------------|-------------|-------------------|------------------------------------------------------------------------------------------------------------------|
| CR Vlaming Head <sup>2</sup>     | 3.0–3.4       | 125.4       | Single age        | Not reported                                                                                                     |
| CR Tantabiddi Bay <sup>2</sup>   | 1.2–1.3       | 124.3       | Single age        | Not reported                                                                                                     |
| CR Mangrove Bay <sup>2</sup>     | 1.4–1.8       | 116–119     | 3                 | Not reported                                                                                                     |
| CR Mowbowra Creek <sup>2</sup>   | 2.5–2.9       | —           | —                 | Not reported                                                                                                     |
| CR Yardie Creek <sup>2</sup>     | 2.6–3.4       | 120–122     | 2                 | <i>Goniastrea</i> , <i>Porites</i> , <i>Faviidae</i>                                                             |
| CR Sandalwood Penin <sup>3</sup> | 1.5–2.0       | —           | —                 | <i>Goniastrea</i> , <i>Hydnophora</i> , <i>Favia</i> , <i>Favites</i> ,<br><i>Lobophyllia</i> , <i>Platygyra</i> |
| SB Tetradon Loop <sup>4</sup>    | 1.5–2.5       | 125–129     | 4                 | <i>Platygyra</i> , <i>Porites</i> , <i>Galaxia</i>                                                               |
| SB Pelican Island <sup>4</sup>   | <0–1.0        | 120–123     | 3                 | Not reported                                                                                                     |
| Cape Cuvier <sup>4</sup>         | 5.0–9.0       | —           | —                 | <i>Acropora humilis</i> (T), corallines (E), coralline cap (10 cm)                                               |
| HA Turtle Bay <sup>5</sup>       | 3.0–4.0       | 124         | 0                 | <i>Acropora</i> (rB, T), <i>Platygyra</i> , <i>Favites</i> , <i>Goniopora</i>                                    |
| HA Rat Island <sup>5</sup>       | 2.0 3.0       | 124         | Single age        | Not reported                                                                                                     |
| HA Roma Island <sup>5</sup>      | 2.0 3.0       | —           | —                 | Not reported                                                                                                     |
| Burney Point <sup>2,6</sup>      | 3.1           | 122–124     | 2                 | <i>Acropora</i> (rB), collapsed thicket                                                                          |
| Leander Point <sup>1</sup>       | ~3            | 122–124     | 2                 | Not reported                                                                                                     |
| Rottneest Island <sup>1,7</sup>  | 3.02          | 125–127     | 2                 | <i>Acropora</i> (B, T) corallines (E). Sub: <i>Goniastrea</i> ,<br><i>Pocillopora</i> sp.                        |
| CL Foul Bay <sup>8</sup>         | 2.0–2.5       | 125–128     | 3                 | <i>Goniastrea</i> sp.                                                                                            |

Column 1: Cape Range (CR), Shark Bay (SB), Houtmann Abrolhos (HA), Cape Leeuwin (CL). References: 1, Stirling et al. (1995); 2, Stirling (1998); 3, Greenstein et al. (2005); 4, O'Leary et al. (2008a, b); 5, Eisenhauer et al. (1996); 6, Johnson et al. (1995); 7, Playford (1988); 8, McCulloch and Mortimer (2008). Column 3: Strictly reliable (SR) ages range defined by initial  $^{234/238}\text{U}$  of  $149 \pm 4$  per mil. Column 4: Stratigraphically consistent (SC) age range from strictly reliable, in-place corals within a conformable section within 3 m of each other, and with an age variation of ~2,000 years or less. Column 6: T, tabular; E, encrusting; B, branching; rB robust branching. Note: Age variation in Holocene reefs is <1,000 years for conformable 3 m intervals of framework (i.e., 3 m is the amount of reef accretion that can occur in 1,000 years; Edinger et al., 2007). For the LIG therefore, age variation should not exceed ~2,000 years (1,000 years  $\pm$  1,000 year analytical error).

adopting the more conservative ratio of  $149 \pm 4$  per mil which is considered by others to be “strictly-reliable” (Gallup et al., 1994; Stirling et al., 1998). Also, only two exposures of in-place coral framework were dated, and both returned a large spread of ages that are inconsistent with limited stratigraphic interval of reef accretion. The other ages reported by Muhs et al. (2002) are from coral storm-gravel deposits and their stratigraphic consistency cannot therefore be assessed. But of the 16 ages in the entire data set with strictly reliable initial ratios, 11 fall within the more restricted interval of 123–118 ka, suggesting a much narrower time window for highstand reef development than claimed by Muhs et al. (2002). These more reliable data are fully consistent with the orbital forcing of climate during the LIG (Muhs, 2002).

### Summary and conclusions

The age, elevation, and architecture of fossil reefs from both uplifted and stable terrains provide key insight into the timing, duration, and nature of the LIG. Uplifted areas provide an assessment of the timing of postglacial SL rise (or glacial termination) and the duration of the interglacial but, due to the tectonic overprint and the possibility of coseismic displacement, it is difficult to infer anything about the detailed SL behavior or the absolute elevation reached during the highstand. By contrast, stable sites can provide a detailed look into the timing and duration of peak interglacial conditions during the highstand, as

well as the absolute elevation and SL behavior during that highstand.

Without doubt, the best studied uplifted reefs of LIG age occur on Barbados and the Huon Peninsula of Papua New Guinea. Reef development on Barbados is well understood largely due to the fact that the relatively simple coral zonation on modern Caribbean reefs is well represented in its fossil counterparts (Jackson, 1992). The uplift of the LIG terrace on the south and west coasts of the island has exposed only the upper ~20 m of reef-crest development and, although earlier workers claimed that reefs were absent until later in the postglacial rise, this is difficult to substantiate now that reefs of late-glacial age have been encountered in submerged cores off the south coast (Fairbanks, 1989). It is much more likely that this 20 m thick reef-crest sequence represents the final back-stepping stage of reef development during the penultimate deglacial SL rise, and that earlier stages are buried beneath subsequent development of interstadial reef terraces (Blanchon and Eisenhauer, 2001). Aside from the incomplete record of reef development, the 20 m-thick reef-crest units display a clear keep-up architecture as demonstrated by their over-thickened facies which retrograde upslope on the west coast and aggrade vertically or prograde on the south coast. The timing and duration of this keep-up reef development, however, has been difficult to substantiate due to subtle diagenetic exchange of U-series nuclides in the fossil corals. This process has produced a 20 ka range of “strictly reliable” coral ages from

135.8 to 115.8 ka which shows little change even when corrected for such open-system effects (Gallup et al., 2002; Thompson and Goldstein, 2005). Yet a continuous 20 m-thick unit of reef-crest corals could develop in a mere 7,000 years using conservative rates of reef accretion, and in as little as 3,000 years at maximum rates. Given the lack of breaks in the reef-crest sequences on Barbados and the large true-age variation between closely spaced samples, it is highly unlikely that this timing or duration is accurate. Indeed, higher precision dating of speleothems has recently shown that Termination II started at 129 ka (Cheng et al., 2009) and implies therefore that the coral ages are inaccurate.

Although the timing and duration of reef development on the Huon Peninsula is similarly afflicted by open-system effects, the greater rates of tectonic uplift have exhumed almost the entire deglacial and interglacial reef sequence. Sections through the upper 30 m of the fossil fringing barrier-reef complex show that the barrier crest and slope facies are over-thickened implying a keep-up response to SL rise. Although supported by an exposure of shallow-water corals 90 m below the barrier crest, the interpretation of a keep-up architecture for the entire sequence is premature because catch-up responses may be obscured by the more complex reef zonation scheme found in the Pacific region. In addition, this complexity has made it difficult to reconstruct the internal architecture of the terrace and delineate separate stages of reef development. In turn, this has led to an unhealthy reliance on radiometric age inversions in establishing reef stratigraphy, and has resulted in ill-conceived claims of double highstands and extreme SL excursions.

There are also two main stable regions around the world where LIG reefs have now been well studied: the southern passive margin of the North-American Plate (Florida, Bahamas, Caymans, and the Yucatan), and the western Australian passive margin of the Indo-Australian Plate (from Cape Range to Cape Leeuwin). Remarkably, all sites in these two regions show almost identical reef development at identical elevations and therefore have likely had identical relative sea-level histories.

LIG sites in these regions show a ubiquitous and extensive stage of reef development that reached +3 m and consisted of reef-crest units with intertidal encrusters, and back-reef and lagoonal patch reefs that in several areas coalesced to form extensive flat-topped units (Yucatan and Florida). The character and elevation of these units is therefore consistent with reef development during a SL stand of +3 m. In Western Australia, these +3 m reefs have a significantly expanded latitudinal range and extend 550 km beyond the modern limit of reef development. This widespread development and expanded range clearly represents the acme of reef development during the LIG. Yet there is compelling evidence to indicate that this +3 m reef stage was abruptly terminated before the next stage commenced and SL rose to its +6 m highstand. This is based on the discovery in all areas (including two of the uplifted sites) of a discontinuous marine-erosion surface

and capping of crustose coralline algae. Most interpretations of this erosion surface, termed the Devils-Point Event, have related it to a transient SL fall of several meters which exposed the reef unit to subaerial conditions for up to 2,000 years. Yet the discontinuous nature of this surface and an absence of any convincing evidence of subaerial exposure or intertidal sculpturing are inconsistent with such an interpretation. An alternative scenario is that it represents a marine-erosion event resulting from a SL jump that drowned the +3 m reefs (Blanchon et al., 2009). This scenario is also supported by reef-surface cap of corallines which implies that reefs died off suddenly while still submerged in the marine environment.

In all areas where the +3 m reefs have been documented, overlying deposits of LIG age clearly indicate that SL subsequently rose from +3 m to its final highstand at +6 m. In most of the areas investigated, however, the overlying sequence is non-reefal and composed of either shallow subtidal sands and beach-derived sand and gravel, or there is no deposition and the +3 m reefal units onlap a bedrock coast with a distinct intertidal notch at +6 m. An important exception to this general sequence, recently reported from the Yucatan, is the discovery of reef back-stepping and reef-crest development up to the final highstand elevation of +6 m (Blanchon et al., 2009). This clearly supports the idea that the SL rise to +6 m was rapid and drowned the +3 m reefs and caused reef back-stepping. But it does not explain why reefs survived and back-stepped in the Yucatan and yet perished in most other areas. A possible explanation might be that the jump to +6 m inundated large coastal tracts in these low-lying terrains and helped establish new sediment-production areas and transport pathways which prevented reef recovery and further development. Such a scenario is supported by sediment-tolerant reef assemblages in the back-reef and lagoonal zones of the +6 m reef in the Yucatan and indicates that even here reef development was not completely normal.

Although confirmation of rapid SL change during the highstand requires duplication of the Yucatan results, there are sufficient data to draw some final conclusions about the timing and duration of the highstand and how it compares with the full interglacial interval. As shown in Table 2, the duration of the LIG as measured from the range of strictly reliable ages in uplifted areas is 136–115 ka. However, very few of these ages are stratigraphically consistent and it is therefore not possible to determine a reliable estimate from these data. The duration of the highstand, as measured in stable areas from the range of strictly reliable ages, is slightly less, between 128 and 116 ka. However, even this reduced range is excessive when the amount of reef accretion is considered. For example, data from the Huon Peninsula indicate that the total amount of accretion during the LIG must have exceeded 90 m, yet reef accretion during the highstand was a mere 6 m. It seems very unlikely that this 6 m of accretion took 12 ka to develop. However, if the stratigraphic context of these samples is considered, and inconsistent



**Last Interglacial and Reef Development, Table 2** Timing and duration of LIG and highstand from reef corals

| Area/reference/time interval          | SR age range (ka [n]) | SC age range (ka [n])   |
|---------------------------------------|-----------------------|-------------------------|
| Barbados <sup>1</sup> LIG             | 135.8–115.8 (11)      | 129.4–123.3 (5)         |
| Huon Peninsula <sup>2</sup> LIG       | 136.0–115.0 (11)      | 133.0–129.9 (3)         |
| N.W. Australia <sup>3</sup> Highstand | 128.9–116.1 (18)      | <b>124.2–119.8 (13)</b> |
| S.W. Australia <sup>4</sup> Highstand | 128.4–125.0 (13)      | <b>128.4–126.9 (11)</b> |
| Hawaii <sup>5</sup> Highstand and LIG | 132.6–115.8 (32)      | 122.1–120.3 (3)         |
| Bahamas <sup>6</sup> Highstand        | 128.4–122.1 (14)      | <b>123.8–122 (10)</b>   |
| Yucatan <sup>7</sup> Highstand        | 125.4–117.0 (5)       | 117–119.5 (3)           |

Column 1: References: 1, Gallup et al. (2002), Thompson and Goldstein (2005); 2, Stein et al. (1993), Esat et al. (1999); 3, Stirling et al. (1995, 1998); 4, McCulloch and Mortimer (2008); 5, Szabo et al. (1994), Muhs et al. (2002); 6, Chen et al. (1991); 7, Blanchon et al. (2009). Column 2: Strictly reliable (SR) ages range defined by initial  $^{234}\text{U}/^{238}\text{U}$  of  $149 \pm 4$  per mil. Column 3: Stratigraphically consistent (SC) age range from strictly reliable, in-place corals within a conformable section within 3 m of each other, and with an age variation of  $\sim 2,000$  years. Note that although Hawaii has the highest number of strictly reliable ages from the highstand, many of these are from coral gravels and their stratigraphic consistency cannot be determined. These ages could be used to determine the LIG duration assuming upslope transport from older reef deposits but it should be noted that ages measured by Szabo et al. (1994) are lower precision.

ages are excluded, the range is reduced to 8 ka from 128 to 120 ka. And in two of the stable areas with the most ages (NW Australia, Bahamas), this range is further reduced to 4 ka from 124 to 120 ka. The only area where a significant number of ages exceed this restricted range is in south Western Australia. Clearly, the possibility exists that even strictly reliable ages that are stratigraphically consistent can be altered by uniform diagenetic exchange of U-series nuclides.

In conclusion, more work is needed on defining the timing of the LIG by dating and documenting basal reef development in uplifted areas. This must include defining the architecture of shallow-water facies to determine if reefs kept pace with SL rise or back-stepped in response to jumps in that rise. For the highstand, more work is needed to document reef architecture in areas where only the 3 m terrace has been identified so that the progression of SL to +6 m can be determined. Finally, order of magnitude improvements in the analytical precision of U-series dating (Cheng et al., 2009) will allow a better assessment of stratigraphic consistency of ages from individual outcrops and should lead to the reconstruction of high-resolution SL curve and resolve conflicts between the timing and duration of the highstand and that of the LIG.

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## Cross-references

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## LOW WOODED ISLANDS

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## Definition

Low Wooded Islands: A distinct type of reef island that occupies a reef platform surface and comprises three distinct biogeomorphic units: a windward shingle island or gravel ridges, a leeward sand island, and a central reef flat zone comprising mangrove.

## Introduction

The term “low wooded island” was introduced by Steers (1929, 1937, 1938) and Spender, (1930) to describe islands with a unique complexity of morphological and biological characteristics. The name is somewhat ambiguous with Spender (1930) preferring “island reef” and Fairbridge and Teichert (1947) suggesting “low wooded island reef”. Despite these differences in terminology, the descriptor “low wooded island” has become firmly established within scientific literature.

A synthesis of the largely descriptive accounts of low wooded islands allows their global distribution to be identified. The geographic location of these islands includes: the northern Great Barrier Reef (Steers, 1929), although Neil (2000) describes an analogous feature in Moreton Bay several hundred kilometers south of the Great Barrier Reef, the Indonesian reef archipelago including Jakarta Bay and the Java Sea (Umbgrove, 1928; Tomascik et al., 1997), Pigeon and Salt cays, Jamaica (Steers and Lofthouse, 1940), and the Belize barrier reef (Stoddart, 1965). Islands

consisting of gravel seaward ridges, leeward sand ridges, and central mangrove filled lagoons are also found on the peripheral rim of some mid-ocean atolls. However, because these latter islands are a component of a larger reef structure, with lagoons and numerous other types of islands, they are not considered low wooded islands.

Detailed descriptions of low wooded islands show that there are differences in morphological expression of biogeomorphic units between reef settings. Stoddart (1965) termed the Belize examples “moat islands” due to their morphological simplicity compared to those from the Great Barrier Reef, which are considered to have the greatest topographic complexity (Stoddart, 1965; Stoddart et al., 1978a). Much of the detailed understanding of the morphological components, sedimentology and evolution of low wooded islands is due to investigations in the northern Great Barrier Reef. This work was the result of two Royal Society Expeditions in 1929 and 1973, which produced comprehensive maps and descriptions of many islands. As a result of this intense scientific effort low wooded islands have become synonymous with the subset of 34 reef platform islands in the northern Great Barrier Reef. The data from these early investigations of low wooded islands have been collated and synthesised by Hopley (1982) and Hopley et al. (2007).

### Geomorphic characteristics

Low wooded islands are associated with relatively small reef platforms that range in area from 1 to more than 500 ha. Reef platforms generally have the following properties: high elevation, are located in regions with small tidal range, are sheltered from high-energy oceanic swell, and are in close proximity to mainland coasts.

While the basic distinguishing features of low wooded islands are the three biogeomorphic units, there is considerable variety in the size and morphology of each unit. Indeed, Stoddart et al. (1978a) argue that low wooded islands exhibit the greatest complexity of all reef islands. Typical examples and characteristic features of these islands, based on investigation of the Great Barrier Reef examples, are shown in Figures 1 and 2. These characteristics are described below following a cross-reef sequence from windward to leeward reef platform.

### Emergent reef flat

The reef flat, which is approximately 100 m in width, is emergent at low water levels and is laterally continuous enclosing the reef top (Figure 2a and b). On some islands the central reef top may also be emergent while on others it is an enclosed depression (Stoddart et al., 1978a). Due to the moderate energy environment of low wooded islands algal ridges are absent. Living coral is absent from the emergent reef flat, which is dominated by algae. However, many of these emergent reef flats have moated pools with living microatolls.

### Shingle ramparts

Asymmetric ridges of coral shingle occur parallel to the reef perimeter (Figures 1 and 2a). These ridges have gentle seaward slopes and steep landward slopes indicative of episodic storm-driven landward movement. In planform the inner edge of ramparts are arcuate with occasional shingle tongues extending on the order of 100 m across the reef. Eroding ramparts form basett edges (Figure 2b). Most islands have multiple ramparts, which when coalesced form shingle islands.

### Moats

Shingle ramparts can impound shallow pools on the inner reef flat. Drainage is impeded in the moats with ponded water supporting coral growth above the elevation of corals on the outer reef.

### Platforms or promenades

Conglomerate platform is commonly found on the outer seaward margins of mangrove and shingle ramparts (Figure 2c). Their genesis is related to migration and cementation of ramparts. On the Great Barrier Reef islands two distinct platform levels have been identified and linked to differing sea level stages (Figure 1g). On a number of low wooded islands dead microatolls also outcrop beneath the cemented platforms.

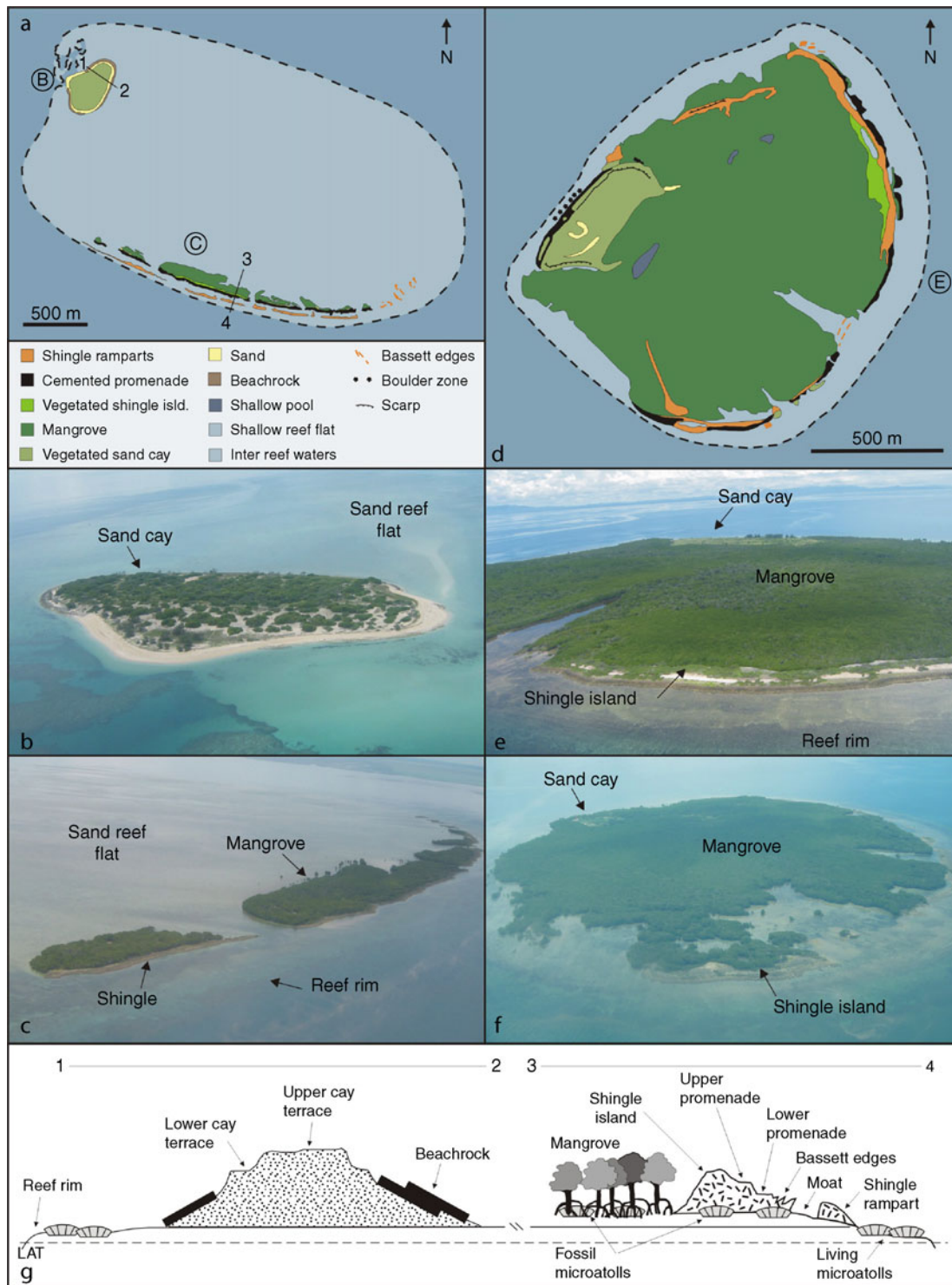
### Shingle islands

Shingle islands are commonly deposited upon the cemented conglomerate platforms. These islands consist of a series of shingle ridges, which may have coalesced, and which are colonised with vegetation (Figures 1 and 2d). The islands vary greatly in width and elevation. Dominant vegetation on these windward shingle islands includes: low mangrove (*Avicennia marina*, *Aegialitis annulata*); succulents (*Sesuvium*, *Salicornia*, *Suaeda*), and salt tolerant *Phemphis* bushes (Hopley, 1982; Stoddart et al., 1978a).

### Mangrove swamp

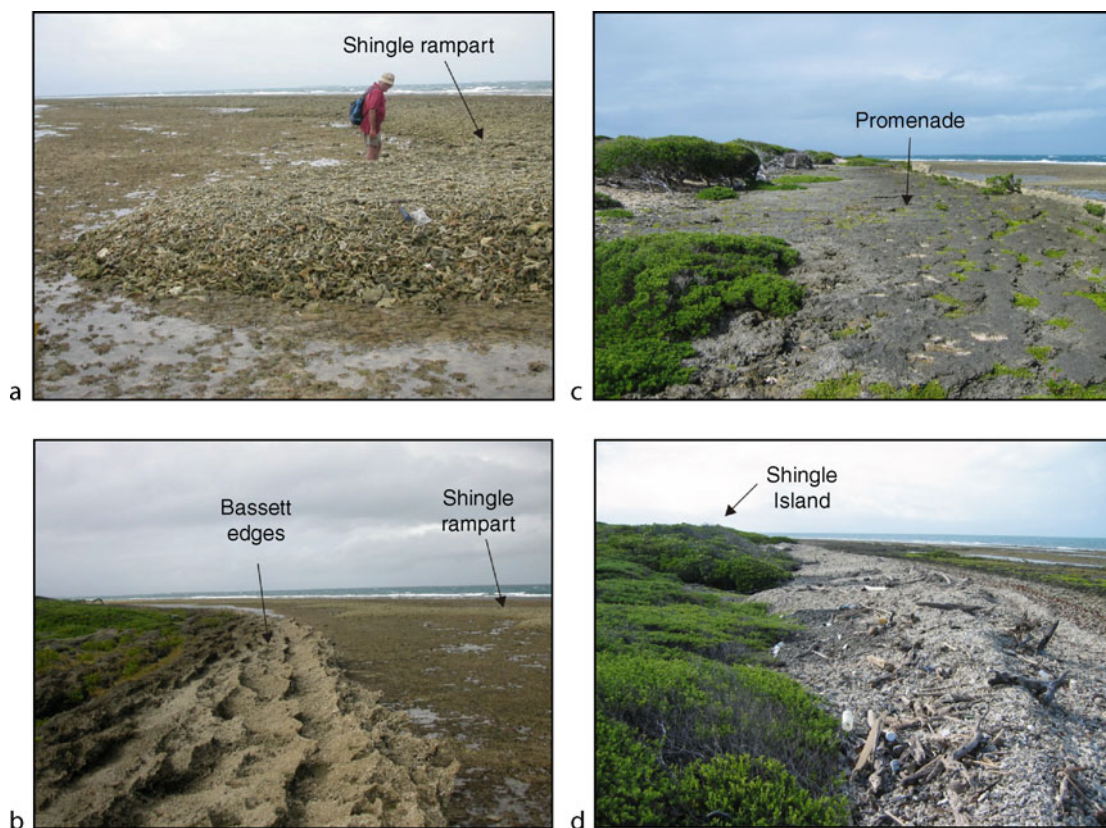
Mangrove communities of varying size occupy the central reef top. Stoddart (1980) recorded 15 species of mangrove from the low wooded islands of the northern Great Barrier Reef. Dominant species include *Rhizophora stylosa* and at higher elevations this is replaced by *Ceriops tagal*, *Bruguiera* sp., *Xylocarpus* sp. and *Osbornia* sp. *Rhizophora* and *Avicennia* are also identified as dominant mangrove species in descriptions of analogous islands on the Belize barrier reef (Stoddart, 1965) and Jamaica (Steers and Lofthouse, 1940).

Mangrove stands vary in extent from 1 to more than 125 ha (in the case of Bewick Island, GBR, Stoddart et al., 1978a). However, there is no relation between reef platform area and proportion of mangrove occupying the reef surface. These communities are considered opportunistic in that their presence and distribution depends on the position and dynamics of shingle ramparts and islands, and the



**Low Wooded Islands, Figure 1** Planform characteristics and geomorphic units of low wooded islands. (a) Ingram-Beanley Island, Great Barrier Reef (after Stoddart et al., 1978a), encircled letters denote position of photographs in (b) and (c); (b) Oblique aerial photograph of Ingram sand cay; (c) Oblique aerial photograph of shingle and mangrove units on Ingram-Beanley Island; (d) Bewick Island, Great Barrier Reef (after Stoddart et al., 1978a, b, c); (e) Oblique aerial photograph of Bewick Island; (f) Oblique aerial photograph of Hannah Island, Great Barrier Reef, all photos by author; (g) Representative cross-section across a low wooded island displaying key biogeomorphic units (after Hopley et al., 2007), indicative location of cross-sections shown in Figure 1a.





**Low Wooded Islands, Figure 2** Photographs of geomorphic features on the windward margin of a low wooded island. (a) Shingle rampart, (b) Bassett edges, (c) Promenade, (d) Shingle island and ridge. All photographs are from Bewick Island and are the authors.

location and elevation of conglomerate and reef topography. In particular, shingle islands and ramparts afford shelter from wave and current energy providing a suitable low energy depositional environment for mangrove colonisation (Stoddart, 1965; Stoddart et al. 1978a).

The substrate underlying mangrove communities varies considerably and includes: sequences of organic mud that reach up to 2 m thick, sandy reef flat sediments, and emergent fields of fossil microatolls (Figure 1g).

#### Leeward sand cay

Supra-tidal sand accumulations occur on the leeward sides of low wooded islands and exhibit greater morphological diversity than ordinary sand cays (Stoddart et al., 1978a). These islands can be grouped according to their location with respect to other reef top geomorphic units, stability and degree of vegetation. In one group, sand cays can occur as discrete and separate features and possess similar characteristics to other reef flat sand cays (e.g., Figure 1a and b). These cays may occur as small, unvegetated and ephemeral features. Others are larger, stable vegetated islands (Stoddart et al., 1978a). These larger islands are commonly covered with woodland or scrub but

have a higher diversity of vascular plants than simple sand cays. A second group consists of discrete vegetated cays, which are surrounded entirely or partially by mangrove (e.g., Figure 1d–f). These islands form contiguous land units with the mangrove and shingle islands and collectively occupy large areas of the reef platform.

A notable feature of the vegetated sand cays of the Great Barrier Reef is the presence of an extensive high terrace surrounded by a lower elevation terrace (Figure 1g). The higher terrace is also distinct from the lower elevation counterpart due to greater soil development, different sedimentary characteristics (McLean and Stoddart, 1978), and more mature and dense vegetation communities. The different terrace levels are indicative of distinct phases of island development.

Stoddart et al. (1978a) note that sand cays have higher numbers of vascular plants than other vegetated cays in the Great Barrier Reef. Typically the higher terrace contains woodland comprising a mix of trees such as *Casuarina equisetifolia*, *Pisonia grandis*, *Pandanus*, *Cordia*, and Coconuts. Common at the fringes of woodland and on lower terraces are shrub species that include *Tournefortia*, *Pemphis*, *Scaevola*, and *Euphorbia* sp. that give islands a bushy appearance (Hopley, 1982).

On some islands lower terraces are characterized by open areas with creepers, herbs, and grasses. Particularly common in the Great Barrier Reef examples are the colonizers *Thuarea lepturus* and *Sporobolus*, the succulents *Sesuvium* and *Portulaca*, and creepers *Ipomoea* and *Canavalia*. A similar range of vegetation has been described from sand cays in the Belize barrier reef and Jamaica (Steers and Lofthouse, 1940; Stoddart, 1965).

### Boulder zone

A boulder zone is a recurrent feature of the leeward reef edge or sand cay shoreline. Reaching up to 4 m in diameter the boulders comprise individual coral colonies of storm deposited origin.

### Formation of low wooded islands

The boundary controls on the formation of low wooded islands are the same as other reef islands. Three factors typically constrain the development of islands. First, a physical foundation is required at or near sea level, which need not be extensive (Hopley, 1997) nor sea level constrained (Kench et al., 2005). Typically this foundation is a reef flat (Stoddart et al., 1978a) although some islands are situated upon lagoonal sediments (Kench et al., 2005). As noted by Stoddart (1965) the reef structure of low wooded islands differs between the Great Barrier Reef and Jakarta Bay. Nevertheless, these structural differences have no influence on island morphology. Second, a supply of sediment derived from the surrounding reef platform is required. Third, a process regime able to entrain, distribute and deposit sediments at different locations on reef surfaces is necessary (Stoddart and Steers, 1977).

The process controls on formation of each biogeomorphic unit are relatively well constrained. Shingle ramparts are considered to be storm wave deposited features with their presence and number on windward reef margins related to storm frequency and the recovery interval of reefs to generate sediment (Stoddart, 1965; McLean and Stoddart, 1978). The storm deposition of gravel deposits has a number of well documented analogues (Scoffin, 1993) such as the formation of sequential island ridges in Lady Elliot Island in the southern Great Barrier Reef (Chivas et al., 1986) and cyclone bank deposition in Tuvalu (Maragos et al., 1973). Sand islands are developed at leeward depocentres on the reef platform at the zone of convergence of swell, which refracts around the reef platform structure and waves that cross the reef flat at high tide. Their development is therefore, controlled by reef platform configuration and orientation with respect to the approach of swell energy and the supply and calibre of sediment on reef flats (McLean and Stoddart, 1978). Of note, the deposition of shingle ramparts disrupts the wave refraction signals propagating across reef surfaces. Consequently, modification of wave processes may have influenced the leeward depocentre and planform configuration of sand cays. It is generally accepted that mangrove colonisation of the central reef flat has occurred under low

energy conditions provided by shingle ramparts, which are conducive to deposition of finer sediments and establishment of mangrove.

Stoddart (1965) proposed a simple process model to account for the presence and distribution of low wooded islands and account for the different formative mechanisms and distribution of depositional products on reef platforms. This model is based on the relative interplay of exposure to wave energy, reef geometry, and sediment calibre. The characteristics of exposure include: variability and wind strength, effective fetch, water depth, and local factors of reef depth, which control incident wave energy. Low wooded islands occur in settings protected from high energy swell. They tend to occur where significant fetch length allows development of moderate wave energy. The moderate energy setting is considered conducive to more fragile branching coral growth forms, therefore, supplying the shingle sediment for ramparts (Steers and Lofthouse, 1940; Stoddart et al., 1978a). Stoddart (1965) concluded that wave action is a sufficient mechanism for both shingle ridge and sand cay formation.

Recognition that the process regime is able to account for the morphological development of low wooded islands has significant implications for the interpretation of regional differences in island morphology. In particular, sea level change can be discounted as a necessary precursor for island formation. However, regional differences in the patterning of Holocene sea level change and reef growth are likely responsible for observed differences in complexity of island morphology.

For example, in the Caribbean, sea level rose continually through the Holocene and slowed significantly over the past 1,000 years (Toscano and Macintyre, 2003). Low wooded islands described from this region have subsequently formed in response to the contemporary process regime at constant sea level position and produced a simple suite of morphological units. In contrast, Holocene sea level in the Indo-Pacific has been at or close to present level for the past 6,000 years with a 1 m highstand approximately 6,000–3,000 years ago (Chappell, 1983). This differing pattern of sea level has imparted a more complicated morphological imprint on low wooded islands.

Results from radiometric dating of reefs and islands in the Great Barrier Reef provides the most detailed dataset with which to place an age framework on the evolution of low wooded islands (Polach et al., 1978; McLean et al., 1978; Stoddart et al., 1978b).

The platforms which support these islands were developed at modern sea level 6,000–5,000 year B.P. Evidence from emergent reef platform and fossil microatolls indicate reef platforms accreted to elevations above present sea level in response to the mid-Holocene highstand. Radiometric ages on high sand cay terraces, beachrock, upper promenades and shingle ridges (Figure 1g) indicate an initial phase of island formation in the period 5,000–3,000 year B.P. with morphological products on the order of 1.0 m above contemporary counterparts.

A second phase of island development has occurred over the past 1,500 years at contemporary sea level producing lower sand cay terraces and shingle ridges. Consequently, the geomorphic complexity of low wooded islands in the GBR results from the long period during which reefs have been close to present sea level combined with distinct changes in sea level position, altering the base level upon which contemporary processes have been able to control island formation.

### Temporal development and morphological change

A number of early studies speculated about the developmental sequence of low wooded islands. Spender (1930) considered the islands to represent equilibrium forms, whereas Steers (1937), on the basis of the width and extent of ramparts suggested, they represented an evolutionary sequence. These ideas were expanded by Fairbridge and Teichert (1947) into an evolutionary sequence in which the increase in extent of mangrove was proposed as an indicator of relative maturity. A similar concept of age development was proposed by Umbgrove (1947) for the islands of Jakarta Bay. Shingle ramparts were observed in different positions across reef platforms and in some cases fused to the sand cay shoreline. Umbgrove (1947) proposed a developmental sequence in which shingle ridges migrate across platforms and fuse with sand islands. Island maturity was therefore linked to the association of shingle ridges with the sand cay.

These early theories of island development were largely based on field descriptions and time-space substitution. However, these models have been largely dispelled based on more detailed consideration of the process regime affecting reefs, the development of chronologies of island formation, and monitoring studies. For example, monitoring of islands in Jakarta Bay by Zaneveld and Verstappen (1952) failed to identify the morphological stages proposed by Umbgrove (1947).

Collectively, these latter studies have also provided a number of insights on the sequence of island development and geomorphic behavior. First, consideration of the process controls on island formation (Stoddart, 1965) and radiocarbon evidence (Polach et al., 1978; McLean et al., 1978; Stoddart et al., 1978b) indicates that shingle ramparts and sand cays may form independently or contemporaneously, but that mangrove colonization logically follows formation of shingle ramparts that afford protection from higher energy wave conditions.

Second, decadal scale monitoring and analysis has identified considerable geomorphic change in low wooded islands which includes: sand cay migration, rampart building, destruction and migration, and mangrove expansion and contraction (Verstappen, 1954; Stoddart et al., 1978c; Rasmussen, 1986; Frank and Jell, 2006). Of note, such changes display no regular or consistent pattern between islands. The principle causative mechanisms of these geomorphic changes are decadal scale variations

in climate (Verstappen, 1954), which reconfigure wave processes on reefs, cyclones, and storms (Moorehouse, 1933, 1936; Stoddart et al., 1978c).

Third, feedbacks are likely to exist that also modify island morphology. Examples include: shingle rampart dynamics modulating mangrove contraction or expansion, the configuration and extent of ramparts controlling wave refraction patterns on reef surfaces and sand cay shoreline processes, and mangrove expansion, which may shut down the process regime influencing shoreline change on sand cays.

Collectively, these observations suggest that each island has its own developmental sequence and ultimate morphological end point, which is determined by its unique combination of location, exposure, reef geometry and size, and sediment calibre, which is then modulated by changes in the boundary process regime.

### Summary

Low wooded islands are a specific and unique type of reef island that occupy the surface of reef platforms. They occur in a number of moderate energy reef settings where the combination of wave energy exposure, reef geometry, and sediment calibre are suitable for island formation. Scientific understanding of low wooded islands is heavily influenced by detailed investigations in the early to mid-twentieth century on islands in the Great Barrier Reef, Australia, recognized as the most geomorphically complex examples. However, since 1973 there have been few detailed studies of evolution or process controls on development of low wooded islands in the Great Barrier Reef or other reef settings. Consequently, global variations in the process regime controlling island development and the precise chronology of island formation are poorly resolved. There remain significant research opportunities to redress these gaps in understanding and develop a global model of the formation and distribution of these distinct island types.

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## Cross-references

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[Conglomerates](#)  
[Coral Cay Classification and Evolution](#)  
[Mangroves](#)  
[Moats](#)  
[Shingle Ridges](#)

## LYELL, CHARLES (1797–1875)

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Born in Edinburgh, Lyell became the dominant geologist of the early nineteenth century with his great three-volume *Principles of Geology*, published during the years 1830–1833. To explain the puzzle of atoll formation, he argued that the circular or oval forms of the numerous coral isles of the Pacific, with lagoons in their center, “naturally suggest the idea that they are nothing more than the crests of submarine volcanos, having the rims and bottoms of their craters overgrown by corals” built by an infinitely slow process on the summits of submerged volcanoes on the ocean floor by “branched madrepores.” In the case of archipelagos and similar distributions, Lyell believed they had been formed from the ejection of volcanic ashes and sand which served as the foundations for yet further reefs.

He also sought to explain the other great question puzzling explorers: why “there should be so immense an area in eastern Oceania, studded with minute islands, without one single spot where there is a wider extent of land than belongs to such islands as Tahiti, Hawaii, and a few others, which either have been, or are still the seats of active volcanoes?” The answer he provided was that

“the amount of subsidence by earthquakes exceeds in that quarter of the globe at present the elevation due to the same cause.” The uniformitarian argument of causes in continuous operation – today known as actualism – was advanced as demonstrative proof: active volcanoes certainly are brief catastrophic events, indicative of the release of subterranean energy, but they remain, none the less, mere transitory epiphenomena on the continuing

elevation and subsidence of the earth’s crust. The Pacific, he reasoned, has simply sunk as the underlying forces have been released, and in corresponding motion the nearby Andes had slowly risen out of the sea, carrying their marine depositions with them.

**Cross-references**

[Darwin, Charles \(1809–1882\)](#)

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## MACNEIL, F. STEARNS (1909–1983)

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Darwin's 1842 model for atoll development provoked numerous alternative ideas including antecedent platforms, eustatic sea level oscillations, and integrated hypotheses. Japanese researchers were the first to consider that modern reefs are growing on limestone platforms exposed to sub-aerial weathering during lower sea level periods of the Pleistocene (Asano, 1942; Yabe, 1942; Tayama, 1952). Their papers, however, were largely ignored or dismissed (e.g., Umbgrove, 1947) until the ideas were redeveloped in the American literature. Initially Stearns (1946) believed that variations in sea level were major factors in producing the relief of atolls and in particular, internal unconformities where the reef limestone was eroded or exposed during low sea levels.

However, the paper published in 1954 by F. Stearns MacNeil of the US Geological Survey has become the most widely quoted source of the hypothesis of an inheritance from sub-aerial forms for the shape of atolls. Interestingly, MacNeil notes that Hoffmeister and Ladd (1944) had previously concluded that the saucer shape of many uplifted Pacific limestone islands was due to solution, and not to the fact that they were raised atolls, yet they did not develop the argument in their exposition on antecedent platforms. MacNeil's theory recognized the importance of organic growth during periods of submergence but placed at least equal importance on the role of solution in fashioning the lagoonal depressions and annular rims of atolls. Case-hardening and development of underground drainage systems were seen as important factors in the development of the sub-aerially exposed limestone

surface. MacNeil, in the introduction to his 1954 paper, stated:

Though it is true that most authors have sought to explain barriers and atolls as the ultimate forms of reefs, the inclusion of all reef hypotheses under one heading implies more conflict than really exists. Generally no distinction is made between theories dealing mainly with the foundation of reefs, and the shape of reefs. There is a general feeling among investigators at present that atolls are not always formed the same way, and therefore no one theory can explain atolls.

and later:

It would seem that each atoll should be studied as an individual and it is not thought that the present hypothesis, believed to be true for the oceanic atolls of the mid Pacific, is necessarily true for the atolls (*sic*) of the Great Barrier Reef.

*MacNeil, 1954. pp. 402–403*

It is possible here that MacNeil was too conservative in his application of his hypothesis, for Purdy (1974) has greatly extended the antecedent karst model to explain the configuration of all reefs by means of preferential reef accretion on topographic highs in underlying subaerially weathered surfaces. However, MacNeil's statements implying that the coral reef problem has been largely a matter of confusing structure and surface morphology, and of assuming that all reefs have a similar evolution, are an illumination of the problem not previously considered. It is from about the time of his paper that general models of reef evolution have become unfashionable, a trend that is noticeable within geomorphology generally, as indicated by Higgins (1975). Higgins attributes this decline in landscape models to a change in the intellectual climate resulting from increasing quantification and interest in process, which in turn have suggested that complex landforms may be explained by more than one hypothesis.



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## Cross-references

[Antecedent Platforms](#)  
[Atolls](#)  
[Darwin, Charles \(1809–1882\)](#)  
[Glacial Control Hypothesis](#)  
[Solution Unconformities](#)  
[Subsidence Hypothesis of Reef Development](#)

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## MAKATEA

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## Definition

*Makatea* is defined originally as an elevated (uplifted) rim of coral reef limestone wholly or partly surrounding a volcanic island. Makatea islands refer to composite islands according to Nunn (1994) as they possess three distinct geomorphic features from the shoreline inwards: a makatea limestone, a depression with swamps and streams, and an exposed volcanic core.

*Etymology*: The term *makatea* was originally defined and used in the southern tropical Pacific (Cook Islands). It derives from the Polynesian language, probably from two words: *maka* (slingstone) and *tea* (white).

*Origin*: The makatea limestone consists usually of Cenozoic reef material, locally with peripheral fringes of Quaternary reef terraces deposited before island uplift (see Montaggioni and Camoin, 1997; Vacher and Quinn, 1997 for reviews). The morphology of makatea islands frequently resembles that of modern barrier reefs or

almost-atolls in which topography is believed to be inherited from pre-existing karstic relief. In most cases, the depression behind the reef rim is the result of subaerial solution by freshwater (Purdy and Winterer, 2006). The final landscape is typified by upland depression-and-rim reliefs and coastal cliffs. The volcanic core has been built by different mechanisms in relation to lithospheric plate tectonics, e.g., hotspot, arc volcanism, and volcanism at or close to divergent plate boundaries. Similarly, uplifting has been controlled by a variety of regional tectonic processes.

*Parent feature*: The island of Makatea in the northwestern Tuamotus (French Polynesia) is a high carbonate, atoll-shaped structure, generally not regarded as a typical makatea island because of the lack of exposed volcanics in its central part. However, its present-day morphology has been produced by uplift of a Cenozoic reef tract, followed by subaerial, karstic erosion. The name of makatea island therefore is suggested to be used in a wider sense and thereby applied to any tropical Pacific island typified by uplifted reefal limestone severely karst-eroded.

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## Cross-references

[Diagenesis](#)  
[Emerged Reefs](#)  
[Solution Processes/Reef Erosion](#)

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## MALDIVES

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## Definition

*Maldives*: The Republic of Maldives is an archipelago of coral atolls and reef platforms located in the central Indian Ocean.

## Introduction

The Maldives archipelago comprises a chain of coral reefs and reef islands situated 700 km southwest of Sri Lanka and positioned between the Lakshadweep Islands (to the north) and Chagos Islands (to the south). The archipelago

extends 868 km from Ihavandhippolhu in the north (6°57'N) to Addu atoll (0°34'S) just south of the equator. Comprising 2,041 reefs the archipelago is globally unique in biological diversity, the diversity of reef structures it possesses, and their mode of evolution. The reef system is host to approximately 1,190 low-lying reef islands. As one of only four atoll nations, the Maldives is commonly regarded as extremely vulnerable to future sea-level and climatic change.

### Early exploration

Earliest scientific investigations of the Maldives involved detailed hydrographic observations of the archipelago by Commander James Moresby 1835–1838. This work produced detailed hydrographic charts of the reef system, which were used by Charles Darwin in constructing his global synthesis of reef evolution, and which remain the most accurate records of bathymetry in the archipelago. At the end of the nineteenth century and beginning of the twentieth century a number of scientific expeditions were undertaken to the Maldives to document the taxonomy and biogeography of reef biota and make observations of oceanographic conditions. Most notable were the expeditions of James Stanley Gardiner in 1899–1900 who undertook the first detailed descriptions of marine and terrestrial fauna and flora as well as reef structures (Gardiner, 1903). Shortly thereafter, Alexander Agassiz also visited the archipelago in 1901–1902 and undertook sampling and description of biological aspects of the reefs (Agassiz, 1903). Seymour Sewell led the “John Murray” expedition to the Maldives (1933–1934) in which Sewell undertook detailed geomorphic observations of a number of atoll islands (Sewell, 1936a, b).

In 1957–1958 the “Xarifa” expedition undertook detailed investigations of the sub-littoral ecology and structure of reefs in many atolls in the archipelago (Hass, 1965). Introducing new systematic survey techniques, this expedition was notable for its taxonomic investigation of faunal and floral communities, identification of high species diversity, and establishment of baseline monitoring locations for future reference of reef community dynamics (Wallace and Zahir, 2007). British scientists also studied the marine and terrestrial geomorphology and ecology of Addu atoll (Stoddart, 1966).

Since these early expeditions the research effort in the Maldives can be described as sparse and narrowly focused on specific aspects of reef ecology, geology, and management. As a result large gaps exist in scientific knowledge and many atolls have not been visited by scientists since Gardiner and Sewell.

### Geologic history

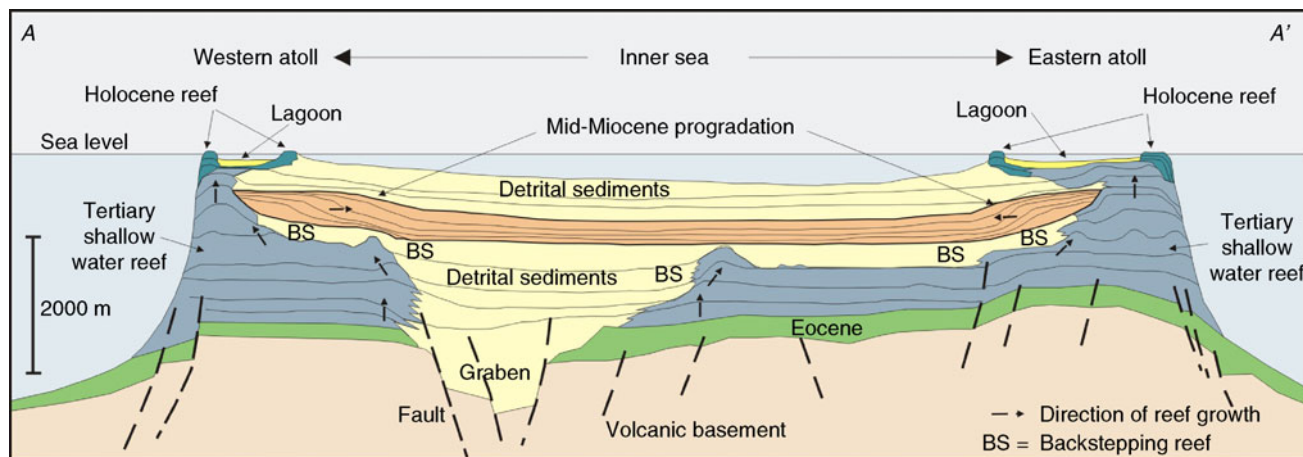
The Maldives constitute the central section of the Laccadives – Maldives – Chagos submarine ridge, which in turn is part of a larger feature that stretches from the early Tertiary Deccan Traps of India to the volcanically active zone of Reunion. The Deccan Traps were the first

manifestation of the stationary mantle hotspot that subsequently produced the volcanic ridge underlying the Maldives. Northward drift of the Indian Plate and northeastward motion of the African plate has resulted in northward age progression along this ridge (Duncan and Pyle, 1988; Duncan and Hargreaves, 1990; Tiwari et al., 2007).

The history of formation of the Maldivian atoll systems differs from the subsidence model proposed by Darwin (1842). Rather, carbonate accumulation through the Tertiary was controlled by phases of aggradation and progradation modulated by large oscillations in sea level (Aubert and Droxler, 1992; Purdy and Bertram, 1993; Belopolsky and Droxler, 2003). The basement rocks underlying the Maldives are Eocene volcanics (55 million years old). These basement volcanics are capped by up to 3,000 m of limestones. Carbonate banks were initiated in the Eocene on topographic highs of the faulted volcanic basin (Figure 1). A number of NNE–SSW oriented grabens acted as channels that became filled with sediments shed from surrounding carbonate banks. The Oligocene to early Miocene were characterized by aggradation of carbonate banks and backstepping in response to sea level rise. An elevated outer rim developed and provided the antecedent structure for the double chain of atolls separated by an inner sea basin that characterizes the central section of the contemporary archipelago (Figure 2). The mid-Miocene (15–10 million years ago) was dominated by lateral progradation from the outer margins of the twin atoll chain toward the inner sea forming a shallow carbonate platform. This period of lateral progradation was followed in the late Miocene and Pliocene by flooding of the platforms and backstepping of the carbonate banks to the periphery of the platform. These peripheral platforms were exposed to karstification during the Plio–Pleistocene sea level minima.

During the Quaternary, the dominant mode of reef development has been vertical coral reef growth on top of these karstified remnants. This vertical reef growth is a consequence of high-amplitude sea-level fluctuations during the Pliocene–Pleistocene, producing alternate periods of exposure and submergence. The Holocene is the last of these reef growth phases.

The contemporary surface morphology of the Maldivian reefs is the result of coral reef growth over the past 10,000 years upon Pleistocene foundations. The Holocene reef growth history of the Maldives has only recently been resolved in detail based on drill cores from Ari and South Maalhosmadulu atolls with the Holocene reef thickness ranging from 12 to 14 m (Gischler et al., 2008; Kench et al., 2009). These studies show the Holocene reef growth initiated approximately 8,100 years ago as sea level flooded the Pleistocene surface. Vertical reef growth occurred at around 7 mm/year for the period 8,100–6,500 years ago and subsequently slowed to 1 mm/year thereafter. Evidence suggests the final stages of reef accretion in the late Holocene exhibited local variations. In situ reef deposits located above sea level on some reefs show



**Maldives, Figure 1** Schematic of the geological structure and evolution of the Maldives archipelago along a west to east transect through the central archipelago. Representative location of transect shown in Figure 2 (after Belopolsky and Droxler, 2003).

vertical reef accretion to a mid-Holocene highstand of approximately 0.5 m above present 2,500 years ago (Kench et al., 2009), where elsewhere the lack of higher sea level evidence suggests reef accretion may have lagged other sites (Gischler et al., 2008).

### Reef structure

The Maldivian archipelago consists of 2,041 individual reefs with a total reef area of 4,513 km<sup>2</sup> (Naseer and Hatcher, 2004). This complex network of reefs is organized into a number of distinct atoll and reef types. There are 21 atolls and 4 oceanic reef platforms.

Atolls can be divided into two types based on their broad physiographic characteristics. *Open atolls* are the dominant atoll type (16 in total) and are characterized by heavily dissected atoll rims, which in planform appear as a sequence of individual reef platforms enclosing a central lagoon. Passages provide free connection between the lagoon and waters of the surrounding ocean and inner sea. Open atolls are large structures ranging from 290 to 3,790 km<sup>2</sup> in area, that contain numerous lagoonal reefs and collectively account for 99.5% of all Maldivian reefs. A striking feature of the open atolls is the presence of faros, ring-shaped coral reefs located within broader atoll lagoons. Globally faros are scarce, yet they are abundant in the Maldives where their formation has yet to be resolved. *Closed atolls* have a near-continuous reef rim that enclose their lagoons, and have limited number of passages connecting the lagoon and surrounding oceanic water. There are only five closed atolls in the archipelago, which are much smaller in area than open atolls, ranging from 47 to 143 km<sup>2</sup>.

Four oceanic reef platforms also occur in the archipelago. These reef platforms are individual reefs that emerge from the inner sea or ocean basin and have no structural connection with neighboring atolls. Oceanic reef

platforms are small in area ranging from 4.4 to 10.2 km<sup>2</sup> and have no lagoon that connects to the open ocean. Vegetated islands occupy a large proportion (16–50%) of the reef platforms.

### Latitudinal gradients in atoll characteristics and processes

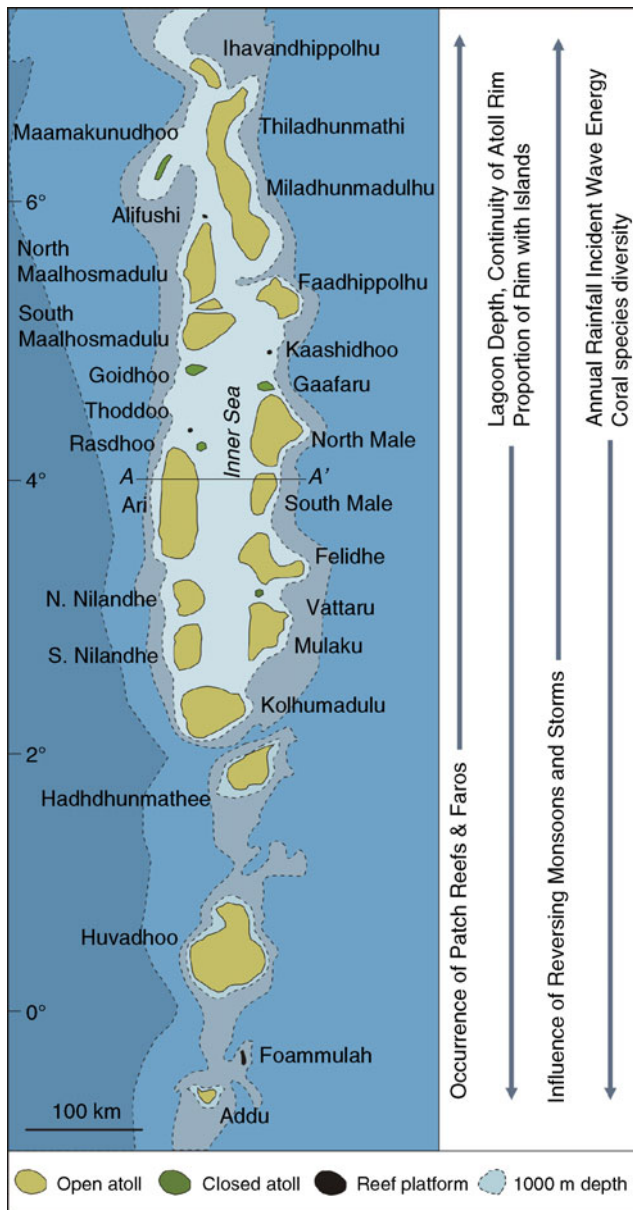
The physical characteristics of atolls in the Maldives show marked spatial variations along the north-south gradient (Figure 2). Northern atolls are characterized by a heavily dissected atoll reef rim, numerous lagoonal patch reefs and faros, and moderate lagoon depths (40–50 m). Reef islands are located on the peripheral and lagoonal patch reefs. Toward the south, atolls are characterized by more continuous atoll reef rims, a higher proportion of peripheral reef rim containing islands, deeper lagoons (70–80 m), and fewer lagoonal patch reefs.

Latitudinal variations in atoll morphology have been attributed to broad north-south gradients in climate and oceanographic conditions. Annual rainfall reduces from south to north along the archipelago (Figure 2). Over the longer-term this rainfall gradient has influenced solutional lowering of lagoons during Quaternary glacial periods. The archipelago is subject to monsoon conditions that switch from the west to northeast in a predictable fashion and influence wave and current patterns. The intensity of oscillating monsoon conditions increases to the north. In contrast, incident wave energy reduces in magnitude in the northerly direction. This energy gradient influences contemporary coral reef growth and island building processes.

### Reef ecology and biodiversity

The central Indian Ocean location of the Maldives places the archipelago close to the mid-point between the reef faunas of the east and west margins of the ocean basin.





**Maldives, Figure 2** Configuration of the Maldives archipelago, central Indian Ocean showing atoll types, names, latitudinal gradients in climate, oceanography, physical atoll characteristics, and coral species diversity.

This geographic position and the fact that the faunal characteristics of the Maldives reefs have close affinities with the Indonesian high diversity reefs and east African reefs is indicative of the archipelago's important role as a biogeographic stepping stone in the so-called "Chagos stricture." As a consequence, the Maldives has high coral diversity with approximately 250 species of scleractinian corals recorded (Pichon and Benzoni, 2007; Wallace and Zahir, 2007). There are also more than 1,200 reef and reef

associated fish species (Rajasuriya et al., 2004). Of note, coral diversity increases southward along the archipelago.

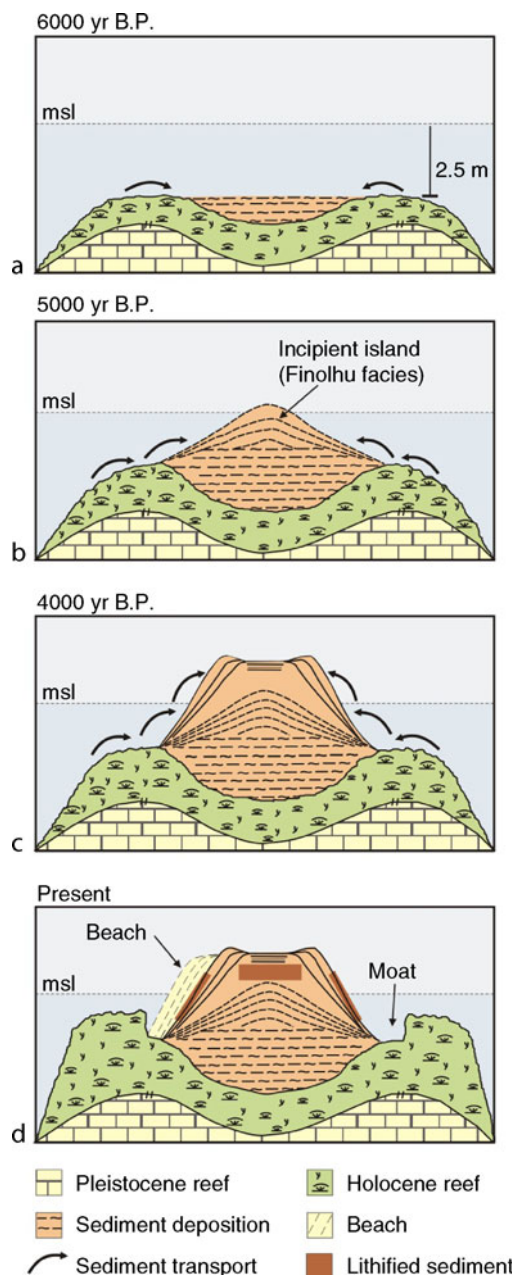
The health of the Maldivian reefs is of critical importance for the maintenance of land, provision of resources (fisheries and aggregates) and economic earnings (tourism). The reef systems are vulnerable to the impact of anthropogenic stresses and global environmental change. Of note, the Indian Ocean-wide bleaching event of 1998 is estimated to have killed upward of 90% of living coral. This observation is based on the monitoring of limited shallow water reef locations (Rajasuriya et al., 2004). Despite localized coral recovery, global climate change and associated sea level rise, increased ocean temperatures and ocean acidification all pose severe threats to reef health in the near future.

### Reef islands

The Maldives contains 1,190 reef islands perched on top of reef surfaces, 200 of which are inhabited. The islands provide the only living space for the Maldivian population of approximately 330,000. Islands are found on peripheral and lagoonal reefs with larger islands located on the peripheral rims of closed atolls. Composed entirely of carbonate sand and gravels derived from the surrounding reef, the islands are typically small and have a mean elevation of less than 1 m above sea level.

Detailed reconstructions of island formation show that the islands are mid-Holocene in age, forming as reefs reached the latter stage of vertical growth through the infill of shallow lagoons (Kench et al., 2005, Figure 3). A major phase of island building occurred 5,500–4,000 years ago across infilled lagoons with islands remaining relatively stable over the past 3,500 years. Following the phase of island building the outer reef has continued to grow, in final stages of catch-up, forming a moat around island shorelines. Although islands are composed largely of skeletal materials derived from the surrounding reef, cemented sediments can occur on the perimeter of islands (beachrock) and in the island core (cay sandstones and phosphate rocks). These lithified sediments indicate a degree of stability to the island core.

The reef islands have been found to exhibit a high degree of short-term variability in response to seasonal climate patterns and extreme events. Island shorelines exhibit rapid morphological adjustments in response to monsoonal reversals in wind and wave patterns (Kench and Brander, 2006). Situated outside the zone of cyclone-genesis, the archipelago and its islands are not subject to extreme storms. However, the archipelago was affected by the passage of tsunami waves as a consequence of the December 2004 Sumatran tsunami. While this event promoted a small amount of island erosion, tsunami waves inundated islands and allowed the transfer of sediments from beaches to island surfaces. This process of overwash was able to vertically build the margins of reef islands by up to 0.3 m providing further



**Maldives, Figure 3** Summary model of the formation of reef platform islands in the Maldives (after Kench et al., 2005).

evidence that the reef islands are morphologically dynamic features on reef surfaces (Kench et al., 2006).

### Summary

Located in the central Indian Ocean the Maldives is one of the largest and most geologically complex mid-ocean atoll chains in the world. The archipelago possesses high biological diversity, a unique geological history, and contains

a diverse range of reef structures and atoll types. The reefs are also host to a large number of vegetated reef islands. However, despite the aerial extent and unique aspects of reef and island diversity, structure and evolution, the Maldives remain one of the least studied reef systems in the world.

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## Cross-references

Atolls  
 Coral Cay Classification and Evolution  
 Faroes Reefs  
 Gardiner, John Stanley (1872–1946)  
 Indian Ocean Reefs

## MANGROVE ISLANDS

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### Definition

“Mangrove islands” is a descriptive term applied usually to overwash banks or outcrops vegetated notably by mangrove plants (cp. Woodroffe, 2002). Considering the geological definition of islands, mangrove islands are atypical since they lack a terrestrial land mass surrounded by water. In the absence of mangrove plants, the base geomorphic feature would be described as a mud bank or sand cay. Therefore, it is the mangroves themselves that give mangrove islands their island-like appearance. The term is sometimes applied more broadly, however, to include other “low” islands with relatively small terrestrial parts amongst the mangroves.

Mangrove islands are a distinct type of island where the bulk of land area, if not all, is below tidal high water. Since mangrove islands depend on mangrove presence, their occurrence is restricted, as are mangroves, to the tropics and subtropics where sea temperatures rarely drop below 20°C, except in Australia and New Zealand (see *Mangroves*). In addition, the substrate of mangrove islands varies widely, including banks of fine estuarine mud, peat, sheltered sandy berms, rocky outcrops, and coral reef enclaves (e.g., see, Hopley, 1982; Duke et al., 1998; Macintyre et al., 2004). While mangroves favor soft sediments and nutrients in sheltered conditions, they can be

very adaptable, clinging tenaciously to hard or soft substrate in periodically exposed locations.

The biodiversity and structural complexity of vegetation on mangrove islands is influenced by global and regional factors (Duke et al., 1998). Overall, mangrove assemblages are comprised chiefly of downstream marine species: in the Indo-West Pacific (see Duke and Larkum, 2008) – *Aegialitis annulata*, *Avicennia marina*, *Bruguiera gymnorhiza*, *Lumnitzera racemosa*, *Osbornia octodonta*, *Pemphis acidula*, *Rhizophora stylosa*, *Rhizophora mucronata*; and in the Atlantic East Pacific (see Tomlinson, 1986) – *Avicennia germinans*, *Conocarpus erectus*, *Laguncularia racemosa*, *Rhizophora mangle*. Specific diversity depends on terrigenous catchment and annual rainfall, reflecting the importance of fresh water. In general, the larger the catchment water supply, the greater the number of mangrove species. So, larger islands often have greater numbers of mangrove species.

There are two predominant types of mangrove islands, as distinct from continental or oceanic islands. Mangrove islands are influenced by sea level, substrate type, and geomorphic setting, to form as either: (1) reefal mangrove islands based on carbonate or peat sediments (Hopley, 1982; Macintyre et al., 2004), clear waters, and low nutrients; or (2) river mouth mangrove islands (Duke et al., 2005) based on fine terrigenous sediments, turbid waters, and runoff nutrients. Both settings are characterized by active processes where over time the tidal banks are continually formed, eroded, and reformed. Reefal mangrove islands form when mangroves grow on coral reef flats or behind shingle ramparts. Low energy conditions may arise within exposed locations. On Australia’s Great Barrier Reef, “low wooded islands” with mangroves (Hopley, 1982), like Low Isles (Figure 1), often occur behind shingle ramparts on windward, southeastern shores of reefs. Mangrove islands form Montgomery Island in northern Western Australia, and they show that tidal range can be extreme, to 10 m. Overall, the height of mangrove stands on coral reefs is usually modest to low, below 5 m. River mouth mangrove islands form when mangroves occupy depositional banks downstream in the mouths of river-influenced estuaries. Low energy conditions occur during seasonal lulls in river flow and storms. Mangroves readily colonize fine deltaic sediments, rich in organic matter, washed in nutrient-loaded river runoff. The height of resulting mangrove trees is maximal, in some cases attaining 50 m; for example, at the mouth of the Mahe River, Darien, Pacific coast of Panama, and Central America. Because these mangrove islands are formed from riverine sediments, their number and size have expanded greatly following the clearing and disturbance of catchment vegetation, as seen in the Fitzroy River estuary northeastern Australia (Duke et al., 2005; see Figure 2).

Mangrove islands provide valuable structure and habitat, plus areas of respite and refuge, for key groups of





**Mangrove Islands, Figure 1** Expanding mangrove island on the coral reef of Low Isles, northeastern Australia, in 2008 – home to threatened Torres Strait Pigeons.



**Mangrove Islands, Figure 2** Mangrove islands double in area over the last three decades in the river mouth of the Fitzroy River, northeastern Australia, in 2004.

displaced coastal fauna, including: insects, fish, crustaceans, molluscs, birds, flying foxes, and other bats. In northeastern Australia, river mouth mangrove islands are the last refuge for flying fox colonies (Hall and Richards, 2000). In the same region, Torres Strait pigeons take refuge on the reefal mangrove island at Low Isles (Crome, 1975; Frank and Jell, 2006).

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## MANGROVES

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### Synonyms

Mangrove forest; Mangrove swamp; Mangrove trees; Sea trees; Tidal forest; Tidal swamp; Tidal wetland

### Definition

**Mangroves.** A tidal habitat comprised of salt-tolerant trees and shrubs. Comparable to rainforests, mangroves have a mixture of plant types. Sometimes the habitat is called a tidal forest or a mangrove forest to distinguish it from the trees that are also called mangroves.

**Mangrove.** A tree, shrub, palm, or ground fern, generally exceeding 0.5 m in height, that normally grows above mean sea level in the intertidal zone of marine coastal environments and estuarine margins.

**Tidal salt marsh.** Small shrubs or herbaceous plants, generally less than 0.5 m in height, that normally grow above mean sea level in the intertidal zone of marine coastal environments and estuarine margins.

**Tidal salt pan.** Flat areas of fine sediments lacking macrophyte vegetation above mean sea level in the intertidal zone of marine coastal environments and estuarine margins.

**Tidal wetlands.** The combination of mangroves, tidal salt marsh, as salt pan, as habitats distinctly occurring between mean sea level and the highest tides. In arid and cooler settings, mangroves share this tidal niche, or are replaced with

diminutive halophyte cousins, the tidal saltmarsh, and flat salt pan expanses with their remarkable microalgal carpet.

### Introduction

Mangroves are one of the world's dominant coastal ecosystems comprised chiefly of flowering trees and shrubs uniquely adapted to marine and estuarine tidal conditions (Tomlinson, 1986; Duke, 1992; Hogarth, 1999; Saenger, 2002; FAO, 2007). They form distinctly vegetated and often densely structured habitat of verdant closed canopies (Figure 1) cloaking coastal margins and estuaries of equatorial, tropical, and subtropical regions around the world (Spalding et al., 1997). Mangroves are well known for their morphological and physiological adaptations coping with salt, saturated soils, and regular tidal inundation, notably with specialized attributes like: exposed breathing roots above ground, extra stem support structures (Figure 2), salt-excreting leaves, low water potentials and high intracellular salt concentrations to maintain favorable water relations in saline environments, and viviparous water-dispersed propagules (Figure 3).

Mangroves have acknowledged roles in coastal productivity and connectivity (Mumby et al., 2004), often supporting high biodiversity and biomass not possible otherwise. Mangrove ecosystems are key sources of coastal primary production with complex trophic linkages (Robertson et al., 1992), as nursery and breeding sites of marine and arboreal life (Figure 4), and as physical shelter and a buffer from episodic severe storms, river flows, and large waves.

In tropical waters, mangrove stands are often sandwiched between two of the world's iconic ecosystems of coral reefs and tropical rainforests. Biota-structured ecosystems, like these, play a unique role in coastal ecosystem processes via a combination of well-developed linkages, coupled with transient biota uniquely adapted to unusual and often dramatic physico-chemical gradients. Linked and dependent relationships developed over millennia have become vital to the survival of each biome. Colonial corals flourish in shallow warm seas of coasts where mangroves buffer and protect them from land runoff. Mangroves absorb unwanted nutrients and turbid waters stabilizing otherwise smothering water-borne sediments and depositional shorelines. These specialized plant assemblages provide important ecosystem services along with additional acknowledged roles of highly productive habitat and nursery sites. The consequences in disturbing these habitats is likely to have unexpected and far-reaching impacts on neighboring ecosystems and dependent biota (Duke et al., 2007).

### Uniquely mangrove origins and vulnerability

Mangroves are a unique ecological assemblage (Duke et al., 1998), remarkable for their relatively small number of widely distributed flowering plants – evolved mostly post-Cretaceous over the last 60–100 million years. The relatively recent evolution of these plants may explain





**Mangroves, Figure 1** Sinuous channels and tidal wetlands of Missionary Bay, northeastern Australia. Amongst the wide mangrove zones are bare saltpans with saltmarsh patches.



**Mangroves, Figure 2** A forest of exposed, above-ground stilt roots of *Rhizophora apiculata*, Daintree River estuary, northeastern Australia.



**Mangroves, Figure 3** Mature, viviparous propagules of a *Bruguiera gymnorhiza* tree, near Dumbea, New Caledonia.

their comparatively low diversity, but this feature is arguably also related to the harsh environmental conditions defining the niche. Today's mangrove flora includes representatives of at least 21 plant families, testament to the

adaptive success of various phylogenetic lineages venturing into the intertidal zone from upland rainforest ancestors. This small group of highly specialized plants tap rich estuarine nutrients with characteristically shallow





**Mangroves, Figure 4** A cormorant makes use of an eroding edge tree of *Sonneratia caseolaris*, in the upper Daintree River estuary, northeastern Australia.

arrays of below-ground roots bearing distinctively vascular, air-breathing anatomy. Specialized above-ground roots and buttresses further provide exposed air-breathing surfaces and physical support, as well as significant habitat amongst their structure – a characteristic shared with adjacent upland forests and reefal corals.

Ancestral mangrove plants are believed to have reinvaded marine environments in multiple episodes from diverse angiosperm lineages culminating in today's mangrove flora (also Saenger, 2002). Their appearance and evolution appears constrained by key functional attributes essential to their survival in saline, inundated settings where isotonic extremes, desiccation, and hydrologic exposure combine as uniquely harsh constraints on organisms living in the tidal zone, and estuaries. The land–sea interface is a dynamic environment, where subtle changes in climate, sea level, sediment, and nutrient inputs have dramatic consequences for the distribution and health of mangroves. Adding to these, direct human disturbance of mangroves include: eutrophication, dredging/filling, overfishing, and sedimentation. The combined pressures, coupled with global climate change and sea level rise, have led to many healthy mangrove areas becoming endangered communities (Duke et al., 2007). Various rehabilitation projects have shown further that it is extremely difficult to achieve effective, large-scale restoration. Urgent protective measures need to be implemented to avoid further mangroves losses and further degradation of coastal ecosystems.

### Rich and diverse

Mangroves are a diverse group of predominantly tropical trees and shrubs growing in the upper half of the intertidal

zone of coastal areas worldwide (Duke, 1992). They are often mistakenly thought of as a single entity. But, like coral reefs, healthy mangroves are functionally diverse and complex. They also provide essential structure and habitat for a host of marine and intertidal species (Figure 5), comprised of both: residents amongst their dense forest of stems and complex roots, and as visitors with each flooding tide. Mangroves are analogous to tropical rainforests also, where they have foliage canopy habitat for birds, mammals, insects, and other invertebrates. Shared ancestral links underlie many similarities between these plant-structured habitats.

Mangroves are not a genetic entity, but an ecological one (Duke et al., 1998). Mangrove vegetation includes a range of functional forms, including trees, shrubs, a palm, and ground fern. The only plant families comprised exclusively of mangrove taxa are Avicenniaceae and Sonneratiaceae, although this continues to be debated. In Table 1, 77 species of mangrove plants are listed for the world. This number however, is not fixed, and varies with different authors since there are a number of subjective and influential factors, including: doubts surrounding the definition of mangroves; whether to include saltmarsh plants; whether to include mangrove associates; and inconclusive taxonomic description of all taxa.

Amongst the 21 flowering plant genera found in mangroves, there is a relatively high degree of specialization for the tidal wetland habitat. Twelve angiosperm genera are exclusively mangrove while ten others include non-mangrove species. This latter group includes: *Aglaia*, *Barringtonia*, *Cynometra*, *Diospyros*, *Dolichandrone*, *Excoecaria*, *Heritiera*, *Mora*, *Pemphis*, *Tabebuia*, and



**Mangroves, Figure 5** *Terebralia* gastropods devouring a fallen mangrove leaf, near Koumac, New Caledonia.

*Xylocarpus*. For *Pemphis*, this genus has only one upland species located inland as an isolated population on the island of Madagascar. Others show different degrees and types of variation. For instance, distinct hybrids are reported in four genera including *Bruguiera*, *Lumnitzera* (Figure 6), *Sonneratia*, and *Rhizophora* (in Table 1, see species prefixed with “X”). Overall, the diversity of species in these genera is often relatively low, being one or two. These relatively low measures of diversity are believed to be the result of harsh growth conditions present in intertidal habitats. Local and regional environmental factors are believed to play a key role in defining the ecological entity that is mangrove habitat. *Rhizophora* species, the most diverse and dominant genus, often occur at the front of mangroves, fronting the sea or channel, and associated with moderate salinities but not extremes. *Avicennia* species, having a wider salinity tolerance, are notably variable occurring in both frontal and upland stands in the Indo-West Pacific.

### Structural diversity

Mangrove plants characteristically range from trees (like species of *Avicennia* (Figure 7), *Rhizophora* (Figure 2)), to shrubs (species of *Aegiceras*, *Aegialitis*, *Pemphis*, and *Conocarpus*), to the trunkless palm (*Nypa fruticans* (Figure 8)), and ground fern (*Acrostichum*). Trees and shrubs vary further where they might be columnar and erect (*Pelliciera rhizophorae* (Figure 9), *Bruguiera parviflora*), to spreading, sprawling (*Acanthus* spp., *Scyphiphora hydrophyllacea*), and multiple-stemmed

(*Ceriops decandra*). Growth form might also vary within the same species (*Lumnitzera littorea* and *Rhizophora*), having both an erect tree form, and low tangled thicket forms. In general, edge plants (both waterfront and landward) have more lower limbs and foliage, and their stems are laterally sprawling and sinuous, rather than erect and straight. Some species typically form combined closed canopies (*Avicennia marina*, *Rhizophora apiculata*, *Bruguiera parviflora*, *Bruguiera gymnorhiza*, *Camptostemon schultzii*, *Xylocarpus* spp.), while others are commonly found as undercanopy plants beneath the closed canopy (like species of *Aegiceras*, *Cynometra*, *Acanthus*, *Acrostichum*, and *Ceriops decandra*).

Mangroves have notable above-ground breathing roots and shallow below-ground anchoring roots, because their soils are usually saturated and airless. The trees have broad support structures, such as buttresses and sturdy prop roots, because soils are often soft and unconsolidated. Root structures above ground include four types: (1) pneumatophores – pencil-like (*Avicennia* (Figure 7)), erect conical (*Xylocarpus moluccensis*), thinly conical (*Sonneratia alba*), and elongate conical (*Sonneratia caseolaris* (Figure 4) and *Sonneratia lanceolata*); (2) knee roots – thick and knobbly (*Bruguiera*) and thin and wiry (*Lumnitzera littorea*); (3) stilt roots (*Rhizophora* (Figure 2)); and (4) buttresses – sinuous planks (*Xylocarpus granatum*, *Heritiera littoralis*, and *Ceriops* spp., *Pelliciera rhizophorae*), and erect “fins” (*Bruguiera X rhynchopetala*, *Xylocarpus moluccensis*). Roots are used by various fauna, but most notably by burrowing shipworms, mollusks, termites, and crabs.

### Factors influencing mangrove distributions

Mangroves have evolved and flourished in their dynamic setting. While mangroves collectively have specialized morphologies and physiologies, these attributes have limits that vary with individual species. The distributional range of each mangrove species reflects its response to the dominant influencing factors at global, regional, and local scales (Duke et al., 1998).

Where mangroves inhabit tropical and subtropical regions of the world, their presence in higher latitudes is generally constrained by the 20°C winter isotherm in the respective hemispheres (Figure 10). Exceptions to this pattern mostly correspond to the paths of oceanic circulation currents where mangrove distributions are broader on eastern continental margins and more constrained on the west. Present day distribution patterns depend on specialized, water-buoyant propagules of mangroves. Their dispersal is constrained by wide bodies of water and continental land masses. Four major barriers restrict dispersal of warm coastal marine organisms (including mangroves) around the world today, namely: the continents of (1) Africa and Euro-Asia; plus (2) North and South American continents; and the oceans of (3) the North and South Atlantic; plus (4) the eastern Pacific. The relative effectiveness of each of these barriers differ, depending on its

**Mangroves, Table 1** Mangrove species of the world. Families and genera with zero 'Non-mangrove' are exclusively mangrove (modified from Duke et al., 1998)

| Families with mangroves                               | Family relatives of mangrove taxa | Family genera | Mangrove genera                                                                             | Non-mangrove      | Mangrove spp.   | Species of mangroves                                                                                                                                                                                                                                                                                                                                                                                                   |
|-------------------------------------------------------|-----------------------------------|---------------|---------------------------------------------------------------------------------------------|-------------------|-----------------|------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Acanthaceae                                           | Black-eyed Susan, Shrimp plants   | 250–300       | <i>Acanthus</i>                                                                             | 30                | 3               | <i>Acanthus ebracteatus</i><br><i>Acanthus ilicifolius</i><br><i>Acanthus volubilis</i>                                                                                                                                                                                                                                                                                                                                |
| Arecaceae                                             | Palms                             | 200           | <i>Nypa</i> *                                                                               | 0                 | 1               | <i>Nypa fruticans</i> +                                                                                                                                                                                                                                                                                                                                                                                                |
| Avicenniaceae<br>(ex Verbenaceae)<br>(or Acanthaceae) | Grey mangroves                    | 1             | <i>Avicennia</i>                                                                            | 0                 | 8               | <i>Avicennia alba</i><br><i>Avicennia integra</i><br><i>Avicennia marina</i><br><i>Avicennia officinalis</i><br><i>Avicennia rumphiana</i><br><i>Avicennia bicolor</i><br><i>Avicennia germinans</i><br><i>Avicennia schaueriana</i><br><i>Dolichandrone</i><br><i>spathacea</i><br><i>Tabebuia palustris</i>                                                                                                          |
| Bignoniaceae                                          | Trumpet-tulip tree, Jacarandas    | 120           | <i>Dolichandrone</i>                                                                        | 9                 | 1               | <i>Tabebuia palustris</i>                                                                                                                                                                                                                                                                                                                                                                                              |
| Bombaceae<br>(or Fabaceae)                            | Baobab, Balsa, Kapok, Durian      | 31            | <i>Tabebuia</i><br><i>Camptostemon</i>                                                      | 245<br>0          | 1<br>2          | <i>Camptostemon philippinense</i><br><i>Camptostemon schultzei</i><br><i>Cynometra iripa</i><br><i>Mora oleifera</i>                                                                                                                                                                                                                                                                                                   |
| Caesalpiniaceae<br>(or Fabaceae)                      | Cassia, Tamarind, Legume          | 150           | <i>Cynometra</i><br><i>Mora</i>                                                             | 70<br>19          | 1<br>1          | <i>Lumnitzera littorea</i><br><i>Lumnitzera racemosa</i><br><i>Lumnitzera X rosea</i><br><i>Laguncularia racemosa</i><br><i>Conocarpus erectus</i>                                                                                                                                                                                                                                                                     |
| Combretaceae                                          | Combretum, Quiquialis             | 20            | <i>Lumnitzera</i><br><br><i>Laguncularia</i><br><br><i>Conocarpus</i><br><i>Diospyros</i> * | 0<br><br>0<br>400 | 3<br><br>1<br>1 | <i>Excoecaria agallocha</i><br><i>Excoecaria indica</i><br><i>Barringtonia racemosa</i><br><i>Pemphis acidula</i>                                                                                                                                                                                                                                                                                                      |
| Ebenaceae                                             | Ebony, Persimmons                 | 3             | <i>Excoecaria</i>                                                                           | 35–40             | 2               | <i>Aglaiacucullata</i><br><i>Xylocarpus granatum</i><br><i>Xylocarpus moluccensis</i><br><i>Aegiceras corniculatum</i><br><i>Aegiceras floridum</i><br><i>Osbornia octodonta</i>                                                                                                                                                                                                                                       |
| Euphorbiaceae                                         | Castor oil, Spurges               | 300           | <i>Barringtonia</i> *                                                                       | 40                | 1               | <i>Pellicierarhizophorae</i><br><i>Aegialitis annulata</i><br><i>Aegialitis rotundifolia</i><br><i>Acrostichum aureum</i><br><i>Acrostichum speciosum</i><br><i>Acrostichum danaeifolium</i><br><i>Bruguiera cylindrica</i><br><i>Bruguiera exaristata</i><br><i>Bruguiera gymnorhiza</i><br><i>Bruguiera hainesii</i><br><i>Bruguiera parviflora</i><br><i>Bruguiera X rhynchoptala</i><br><i>Bruguiera sexangula</i> |
| Lecythidaceae                                         | Brazil nuts                       | 15            | <i>Pemphis</i>                                                                              | 1                 | 1               |                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Lythraceae                                            | Crepe Myrtle, Henna, Cuphea       | 25            | <i>Aglaia</i><br><i>Xylocarpus</i>                                                          | 100<br>1          | 1<br>2          |                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Meliaceae                                             | Mahogany, Rosewood                | 50            | <i>Aegiceras</i> *                                                                          | 0                 | 2               |                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Myrsinaceae                                           | Turnip-wood, Mutton-wood          | 35            | <i>Osbornia</i>                                                                             | 0                 | 1               |                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Myrtaceae                                             | Eucalyptus, Bottlebrush, Guavas   | 80–150        | <i>Pelliciera</i><br><i>Aegialitis</i> *                                                    | 0<br>0            | 1<br>2          |                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Pellicieraceae                                        | Tea, Camellia, Franklinia         | 1             | <i>Acrostichum</i>                                                                          | 0                 | 3               |                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Plumbaginaceae                                        | Sea lavender, Thrifts             | 10            |                                                                                             |                   |                 |                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Pteridaceae                                           | Ferns                             | 35            |                                                                                             |                   |                 |                                                                                                                                                                                                                                                                                                                                                                                                                        |
| Rhizophoraceae                                        | Crossostylis, Cassipourea         | 16            |                                                                                             |                   |                 |                                                                                                                                                                                                                                                                                                                                                                                                                        |



Mangroves, Table 1 (Continued)

| Families with mangroves        | Family relatives of mangrove taxa | Family genera | Mangrove genera    | Non-mangrove | Mangrove spp. | Species of mangroves                                                                                                                                                                                                                                                                                                                                                                                        |
|--------------------------------|-----------------------------------|---------------|--------------------|--------------|---------------|-------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
|                                |                                   |               | <i>Ceriops</i>     | 0            | 4             | <i>Ceriops australis</i><br><i>Ceriops decandra</i><br><i>Ceriops tagal</i><br><i>Ceriops zippeliana</i>                                                                                                                                                                                                                                                                                                    |
|                                |                                   |               | <i>Kandelia</i>    | 0            | 2             | <i>Kandelia candel</i><br><i>Kandelia obovata</i>                                                                                                                                                                                                                                                                                                                                                           |
|                                |                                   |               | <i>Rhizophora</i>  | 0            | 11            | <i>Rhizophora</i><br><i>X annamalayana</i><br><i>Rhizophora apiculata</i><br><i>Rhizophora</i><br><i>X lamarckii</i><br><i>Rhizophora mucronata</i><br><b><i>Rhizophora samoensis</i></b><br><i>Rhizophora X selala</i><br><i>Rhizophora stylosa</i><br><i>Rhizophora</i><br><i>X tomlinsonii</i> *<br><i>Rhizophora mangle</i> +<br><i>Rhizophora racemosa</i><br><i>Rhizophora</i><br><i>X harrisonii</i> |
| Rubiaceae                      | Coffee, Gardinia, Quinine         | 500           | <i>Scyphiphora</i> | 0            | 1             | <i>Scyphiphora hydrophylacea</i>                                                                                                                                                                                                                                                                                                                                                                            |
| Sonneratiaceae (or Lythraceae) | Duabanga                          | 2             | <i>Sonneratia</i>  | 0            | 9             | <i>Sonneratia alba</i><br><i>Sonneratia apetala</i><br><i>Sonneratia caseolaris</i><br><i>Sonneratia griffithii</i><br><i>Sonneratia X gulngai</i><br><i>Sonneratia</i><br><i>X hainanensis</i><br><i>Sonneratia lanceolata</i><br><i>Sonneratia ovata</i><br><i>Sonneratia X urama</i>                                                                                                                     |
| Sterculiaceae (or Malvaceae)   | Cocoa, Kola, Bottle trees         | 70            | <i>Heritiera</i>   | 29           | 3             | <i>Heritiera fomes</i><br><i>Heritiera globosa</i><br><i>Heritiera littoralis</i>                                                                                                                                                                                                                                                                                                                           |

Genera marked with an asterisk have been classified previously comprising their own family, named: Diospyraceae, Barringtoniaceae, Aegicerataceae, Nypaceae, Aegialitidaceae, and Pellicieraceae, respectively. Species region codes: regular font refers to those from the Indo-West Pacific; underlined names occur in the Atlantic East Pacific; **bold underlined** occur naturally in both; + indicates species introduced to, and established in, the other region

\*See Duke (2010)

geological history, dispersal/establishment ability, and the evolutionary appearance of respective species.

Regional distribution patterns of mangroves are further influenced by habitat availability and local environmental factors such as rainfall, estuary size, and tides. In Australia (Duke, 2006), two major environmental factors, temperature and rainfall, largely explain regional distributions where low temperatures limit the latitudinal extent of species – affecting the pool of available species. The relative number of species is also highest in areas of higher rainfall. Species richness declines generally with increasing latitude on north-south coastlines and groupings of islands. In general, species diversity in mangrove stands of equal size is greatest in wet equatorial areas. However,

where rainfall is comparable, species diversity is higher in longer estuaries with larger catchments. The influence of rainfall, therefore, not only comes from rain falling directly on mangrove stands, but also as it influences runoff volume from upstream catchments.

At the local scale, individual mangrove species usually occupy only part of an estuary from sea mouth to tidal limit upstream (Duke et al., 1998). Species generally display a preferred estuarine range based on the overall salinity tolerance. For instance, species like *Avicennia marina*, *Rhizophora stylosa*, and *Sonneratia alba* commonly occur in downstream locations. By comparison, *Rhizophora mucronata*, *Sonneratia caseolaris*, and *Bruguiera sexangula* are found upstream in larger,



**Mangroves, Figure 6** Delicate pink flowers of the rare hybrid shrub, *Lumnitzera rosea*, Le Cap River, New Caledonia.



**Mangroves, Figure 8** Erect fruiting bodies of the striking mangrove palm, *Nypa fruticans*, Kien Giang Province, Vietnam.



**Mangroves, Figure 7** Sizing up an ancient tree of *Avicennia germinans*, near Braganza, Amazonian Brazil.



**Mangroves, Figure 9** Attractive flowers of *Pelliciera rhizophorae* support hummingbirds, near Diablo on the Pacific coast of Panama, Central America.

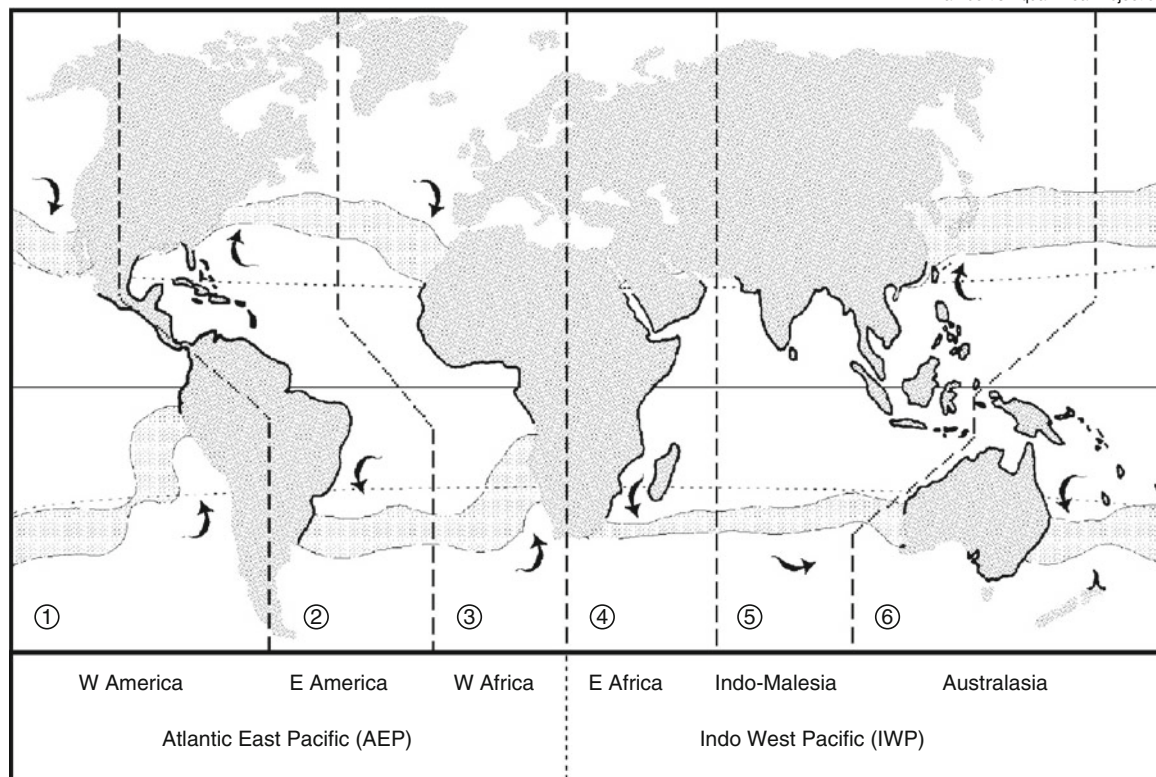
freshwater-dominated estuaries. Furthermore, at this local scale, respective species occupy distinct parts of the tidal profile above mean sea level. Characteristic zonation bands of different mangrove assemblages indicate the

pronounced influences of inundation frequency and tidal elevation. For example, species like *Avicennia integra*, and *Sonneratia alba* commonly occupy low intertidal positions. By comparison, *Heritiera littoralis*, *Xylocarpus granatum*, and *Lumnitzera racemosa* are found in high intertidal positions. Some species, such as *Avicennia*



## Mangrove distribution

Lambert's Equal Area Projection



**Mangroves, Figure 10** World distribution of mangroves (dark line along coastal margins) showing global regions and subregions with ocean zone limits at the seasonal 20°C isotherm (source: Duke et al., 1998).

*marina*, *Acanthus ilicifolius*, and *Aegiceras corniculatum*, are observed at high and low intertidal positions.

the full impact of global climate change and sea level rise begin to take effect.

## Conclusion

Mangroves and tidal wetlands are essential to the sustainability of highly productive natural coastal environments. However, these ecosystems and their dependant biota (Figures 4, 5, and 9) are under serious threat from the escalation this century of large-scale land clearing and conversion of coastal forested wetlands (including mangroves) with the development of coastal lands for agricultural, aquaculture, port, and urban and industrial use (Field, 1995; Duke et al., 2007). In populated areas, key coastal rivers have become little more than drains transporting eroded mud and effluent to settle in downstream estuarine reaches, as well as in shallow embayments and inshore coral reefs. Remaining mangroves have become depauperate, poorly functional vestiges with relatively low resilience. Where healthy, mangrove-lined estuaries had once offered respite and critical dampening of land runoff, in recent years these bastions of coastal buffering and filtering – dubbed “coastal kidneys” – are not responding well to expanding human activities. Efforts to remediate these impacts is being undertaken in many ways with international and regional partnerships, but more is needed as

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## Cross-references

[Coral Cay Classification and Evolution](#)  
[Low Wooded Islands](#)  
[Mangroves](#)

## MARIANA ISLANDS, CORAL REEF GEOLOGY

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### Definition

The Mariana Islands are an arch of volcanic islands stretching ~500 miles from Guam to Uracas. Coral reefs occur only in the volcanically inactive southern part (Figure 1). Most of the human population lives on Guam and Saipan and the political organization is split into the U.S. Territory of Guam and the Commonwealth of the Northern Mariana Islands.

The Marianas are part of the Izu-Bonin-Mariana (IBM) arc system, stretching ~2,800 km from Japan to south of Guam. Modern reef building occurs exclusively in the southern Marianas from Guam to Farallon de Medinilla (Figure 1). Corals also occur in the northern arc but no extensive framework production is reported, likely due to a combination of high latitude and relative tectonic instability. In the southern Marianas, temperatures are tropical and ideal for reef-building organisms. Mean annual air temperatures in Guam are 27°C, with ~6°C variations between daily maxima and minima (Figure 2). Relative humidity ranges 65–80% by day and 85–100% by night (Mink and Vacher, 1997). Long-term annual SST means vary between 28°C and 29°C. Tinian has a mean tidal range of 45 cm and a spring tide range of 65 cm (Doan et al., 1960). Rainfall averages at Guam 85–115 in./year (Gingerich, 2003), at Tinian 43–97 in./year (Gingerich, 2002), and at Saipan 34–145 in./year (Carruth, 2003). Wet and dry seasons are well developed with ~70% of total annual rainfall from July–December. Seasonally pulsed rainfall in combination with steep slopes, lateritic soils and deforestation led to runoff and

sedimentation problems on coral reefs (Wolanski et al., 2003, 2004). The Marianas are influenced by the ENSO, and coral records indicate an ~0.75°C warming over the past two centuries (Asami et al., 2005).

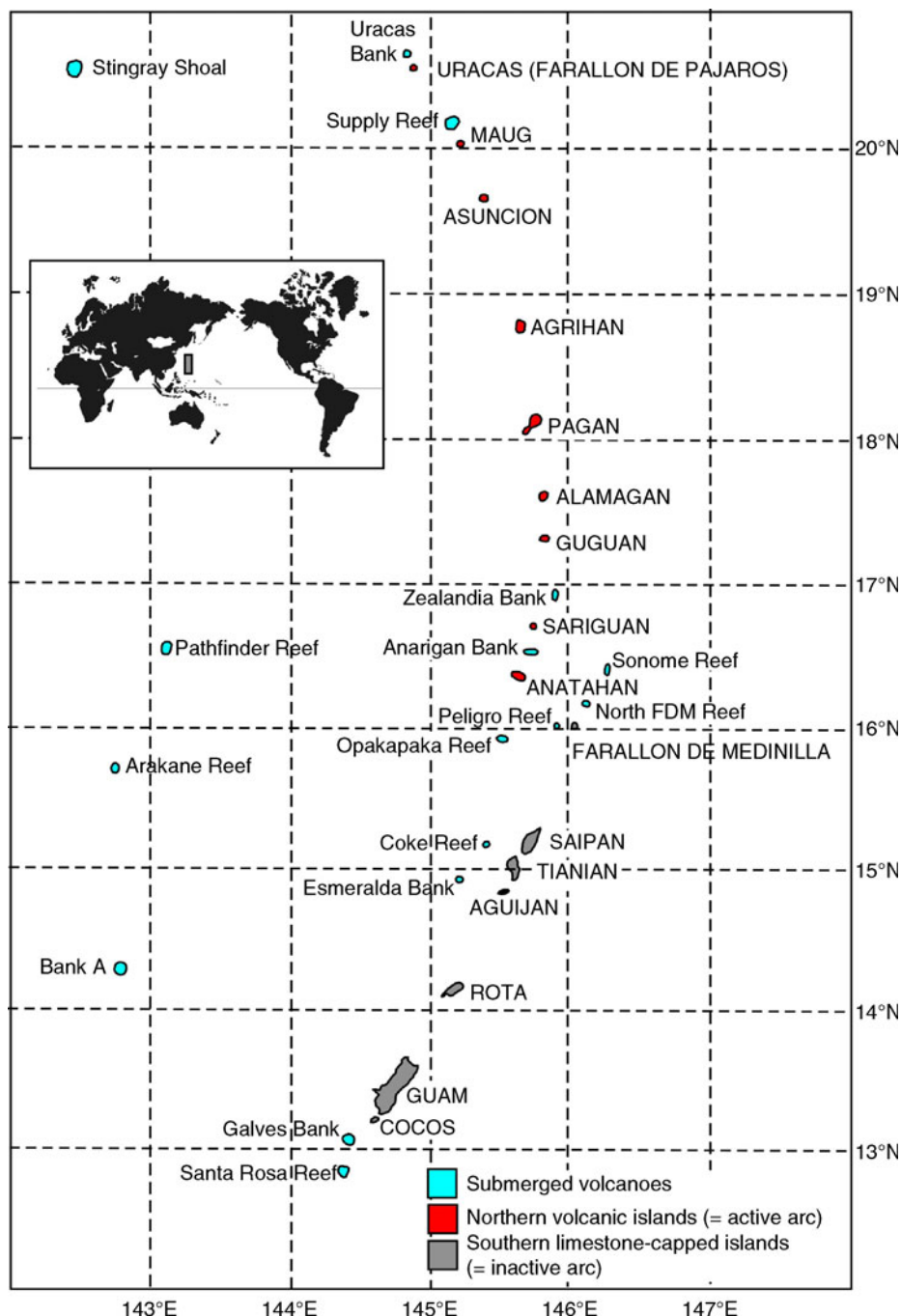
### Holocene coral reefs in the southern Marianas

Two major Holocene reef-building episodes are known in the southern Marianas. An early Holocene episode is found in the Merizo (Guam), Milencatan (Rota) and Tanapag (Saipan) Limestones, and the modern reef (Siegrist et al., 1984b). Present-day coral frameworks are mostly narrow and of the fringing type, their morphology often clearly influenced by underlying morphology. In Guam, many small bays are reef-fringed with rivers entering. In such cases, reefs are discontinuous at the rivermouths and increase in thickness and coral cover away from the rivers (Wolanski et al., 2003, 2004). Two notable exemptions to the general pattern of narrow fringing reefs hugging the islands' shorelines exist in Cocos Lagoon (Guam) and Tanapag Lagoon (Saipan), where barrier reefs occur. Development of these lagoons is structurally controlled. Additionally, fringing reefs are developed along the shorelines inside the lagoons (Emery, 1962; Randall, 1979). Also Tinian had a small section of barrier reef that was filled and dredged into a port during World War II.

Four distinct coral habitats (Figure 3), of which only one involves an actively growing reef, occur in the Marianas (Randall, 1985):

- Habitat I consists of *in situ* reef frameworks, with well-developed buttress and channel system (Pagan, Anatahan, Saipan, Aguijan, Rota, Guam).
- Habitat II occurs among volcanic boulders, *in situ* frameworks are absent or only thin veneers (Pagan, Guguan, Anatahan).
- Habitat III exists primarily between old limestone rocks and boulders, *in situ* frameworks are absent (Aguijan).
- Habitat IV occurs along limestone slopes with few boulders, *in situ* frameworks are absent (Saipan, Rota, Guam).

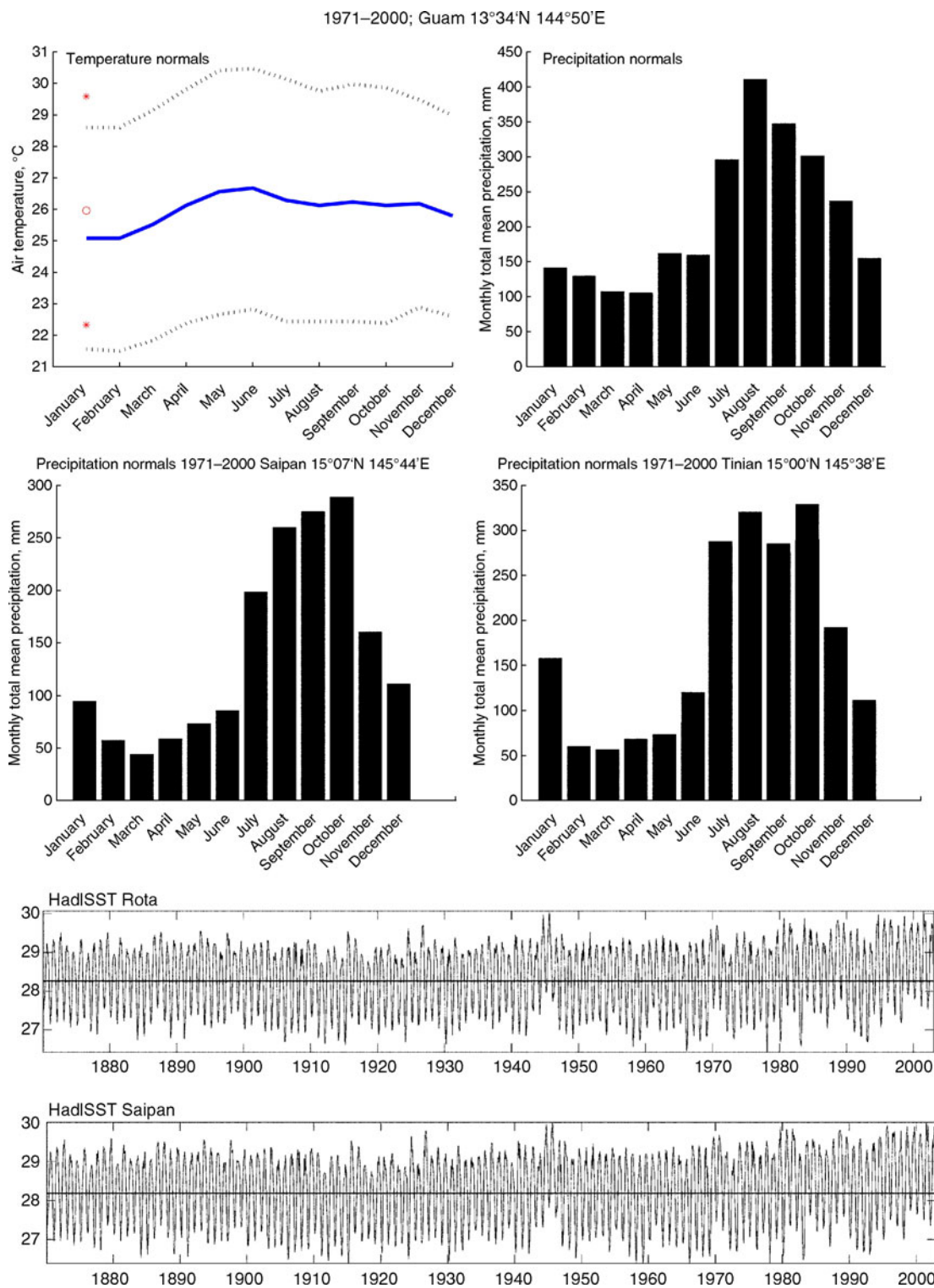
Underlying, and determining the position of late Holocene reef growth are the early Holocene Merizo Limestone (also called “2 m limestone”) on Guam, the Milencatan Limestone on Rota, and the Tanapag Limestone on Saipan. These limestones represent the first phase of reef building in the early Holocene from the post-Wisconsin transgression through the mid-Holocene highstand at ~4,000 year B.P. (before present). They contain beautifully preserved, emergent reef facies in the low supratidal to shallow subtidal and are exposed to about 2–4 m. The emergence of these early Holocene reefs is likely due to tectonic factors (Kayanne et al., 1993; Siegrist and Randall, 1992). Thickness on Guam varies between 5 and 1 m (Siegrist and Randall, 1992). The limestones are coral-dominated and contain virtually all genera that are found in the modern reefs. Growth history on Rota is as follows (Bell and Siegrist, 1988): at 5,500 year B.P. sea level flooded an older, bioclastic facies of the already



**Mariana Islands, Coral Reef Geology, Figure 1** The Mariana Islands, consisting politically of Guam and the Commonwealth of the Northern Mariana Islands, the westernmost territories of the USA.

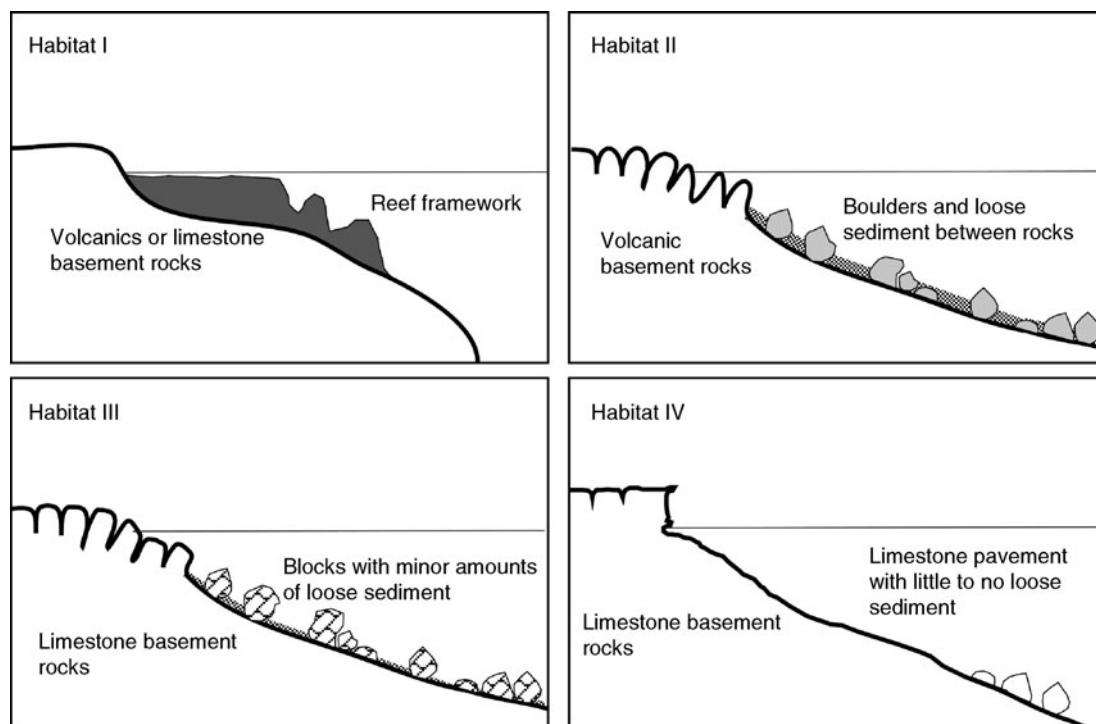
existing Milencatan Limestone and corals settled on preexisting highs about 80 m behind today's reef margin. Between 5,500 and 4,700 year B.P. corals accreted primarily under rising sea-level conditions and produced high buttresses dominated by corymbose *Acropora* and thick algal crusts. Large *Porites* mounds occurred in protected areas. Around 4,700 year B.P. sea-level rise slowed and

the reefs caught up to the surface (then around +2.5 to 3 m above present sea level; Bell and Siegrist, 1988). Maximum sea level was at ~4,200 year B.P. on Rota and Guam (Kayanne et al., 1993; Pirazzoli and Montaggioni, 1988; Dickinson, 2000). Coral frameworks were then encrusted by digitate coralline algae, which Bell and Siegrist (1988) and Kayanne et al. (1993) interpret as



**Mariana Islands, Coral Reef Geology, Figure 2** Atmospheric temperature record and precipitation at Guam, precipitation only at Saipan and Tinian (National Climatic Data Center, NOAA). Normals are uninterrupted measurements for three consecutive decades. Original data were transformed into metric units. Red circle = annual mean; red stars = minima and maxima. Lower two panels: Hadley Center's synthetic HadISST data for Rota and Saipan, as representatives of the southern and northern limestone islands. Lower two panels: Monthly temperature mean, and trend line.





**Mariana Islands, Coral Reef Geology, Figure 3** Generalized vertical profiles of coral habitats. (Modified from Randall [1985] and Siegrist et al. [1991].)

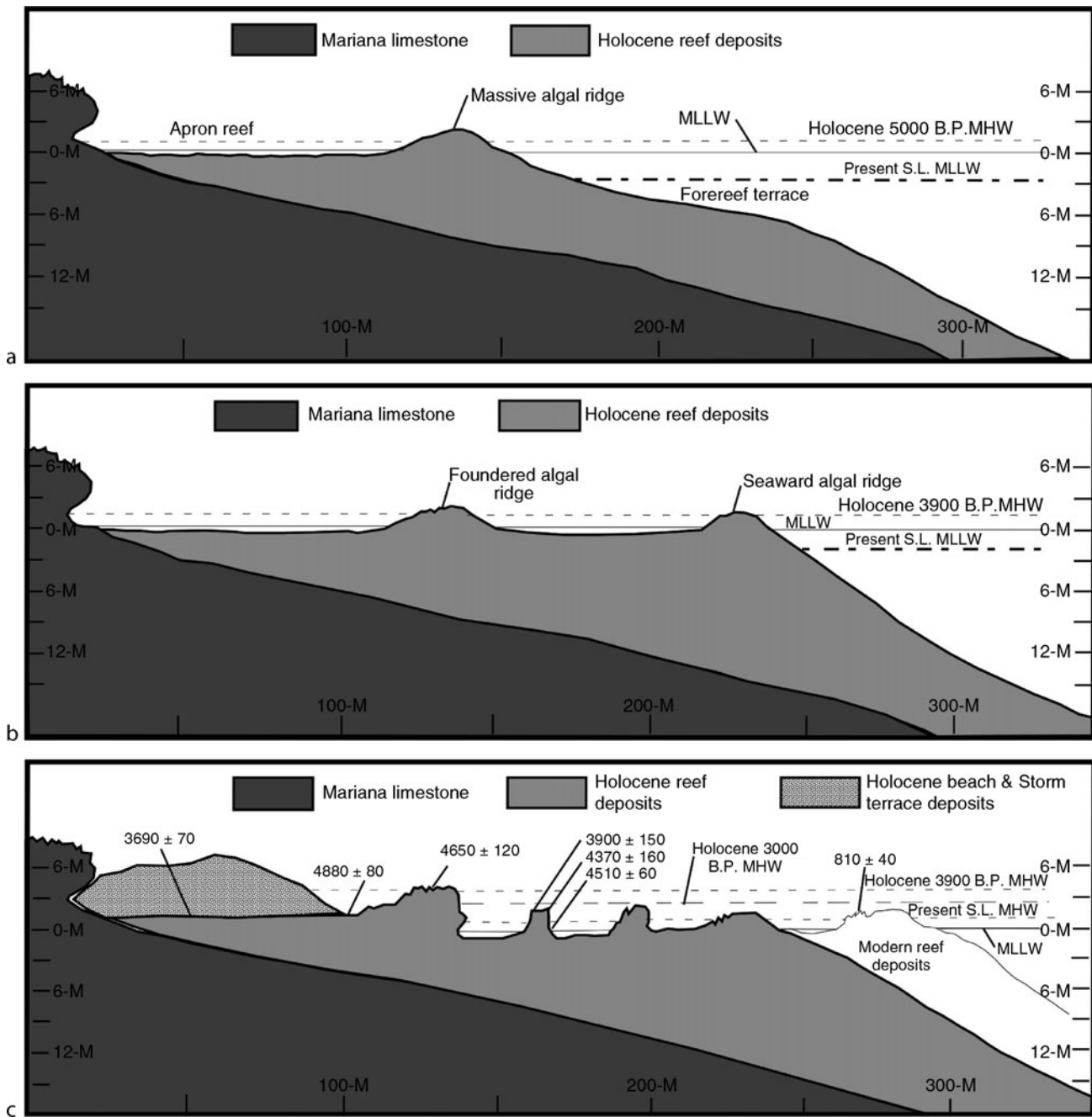
shallow, relatively high-energy facies, that can still be found in the same area today. Between 4,700 and 2,900 yr B.P. sea level fell, exposing the buttresses, and by 2,850 year B.P. corals settled on the present reef flat and the algal ridge began to develop (Figure 4). A total of 45 species, which still occur in the area, are recorded in the Merizo Limestone (Siegrist et al., 1984a; Randall et al., 1984). The dominant corals were corymbose *Acropora* which fueled the rapid growth and aggradation of the reefs. Similar facies were also described from Rota (Bell and Siegrist, 1988): (1) coral framestone facies of corymbose *Acropora* (primarily *A. humilis*; Kayanne et al., 1993) and in leeward settings of *Porites* mounds, considered to be the catch-up phase of reef growth; (2) algal bindstone facies, which are interpreted as the keep-up algal ridge; and (3) detrital facies at the leeward margin of the reef. High-magnesium cements were common besides aragonite cements.

On Guam and Rota, the early Holocene fringing reef (Merizo Limestone on Guam and Milancatan Limestone on Rota) displaced later Holocene reef growth seaward (Kayanne et al., 1993). Early Holocene limestones are well eroded, in particular, in the softer landward, detrital facies behind the corymbose coral facies (Siegrist et al., 1984a), in which deep lagoons can develop. The present-day reef frequently grows in form of well-developed groove-and-spur buttresses. Also the Merizo and Milencatan reefs had well-developed buttresses and it is unclear whether these reflect forcing by antecedent topography and/or wave

energy. Morphology in deeper water frequently is also highly convoluted and in many areas it is evident that the modern reef is forced into its shape.

There are not only similarities in morphology between the early and late Holocene reefs, but also in the distribution and composition of the primary calcareous reef-builders. The same coral species, as listed by Siegrist and Randall (1985) and Randall et al. (1984), for the early Holocene occur today. Modern buttresses on the reef slope are primarily built by corymbose *Acropora* and deeper on the reef slope or in more sheltered areas, large *Porites*- or *Goniastrea*-built buttresses occur. Shallowest and highest energy parts of the reef edge, when not occupied by calcareous algae, show local dominance by *Pocillopora*. The shallowest reef environments in the Merizo and the present-day reefs are covered by a densely calcified algal ridge. Landward of this algal ridge, another zone of corymbose *Acropora* can be found. In lagoons that are eroded into the Merizo or Milancatan Limestone, typically good growth of *Heliopora coerulea* is found in well-drained areas, large stands of open-arborescent *Acropora* occur alongside *Porites* micro-atolls.

A similar zonation is found across the lagoons of Saipan and Guam. The biotic zonation described by Cloud (1959) at Tanapag lagoon is still recognizable despite significant reduction in space covered by corals and sea grasses (Houk and van Woesik, 2008). A reef slope with variable coral cover and groove-and-spurs abuts a well-cemented reef crest that slopes lagoonward and is



**Mariana Islands, Coral Reef Geology, Figure 4** Stages of Holocene reef growth on Guam from Randall and Siegrist (1988). It is clearly visible how strongly the morphology of present-day reef growth is determined by early Holocene reef growth.

densely overgrown with massive corals and corymbose *Acropora*. Areas with large thickets of *Acropora formosa* still occur but cover is dramatically reduced since the 1940s (about 20% of the lagoon shifted from coral and sea grass cover to sand, Houk and van Woesik, 2008). Toward the center of the lagoon, coral growth becomes increasingly sparse as cover by sandy sediment increases. Rocky outcrops with low coral cover and increasingly high

algal cover toward the land as well as small patch reefs occur irregularly in the lagoon. Dense sea grass beds have also been reduced in size (Houk and van Woesik, 2008).

#### General geology of the southern Marianas – volcanics and limestones

Guam, at the southwestern end of the West Mariana Ridge, was volcanically active from 32 to 20 Ma

(= million years) and 9 to 5 Ma (Reagan and Meijer, 1984). Rifting of the West Mariana Ridge created the Mariana Trough and the Mariana Ridge. Volcanic activity resumed ~1.3 Ma in the active, northern, ridge. The main volcanic basement of Guam resulted from the first volcanic phase and is evidenced in the middle Eocene Facpi Formation (~200 m thick boninite lavas with some limestone infills) and the Eocene to early Oligocene Alutom Formation (~400 m thick, tuffaceous shales, sandstones, volcanic breccias, lapilli conglomerates, pillow lavas, tubidites, some calcareous shales in the Mahlac member, and some coral-rich floats, Schlanger, 1964). Serious carbonate sedimentation began in the upper Oligocene/lower Miocene as Maemong Limestone, a member of the Umatac Formation which is of shallow-water origin and consists of mud- to wackestones with coral (*Porites* and *Acropora*) rudstones and intermixed volcanic detritus. Reefal organisms such as corals, *Tridacna*, *Halimeda*, and crustose algae are common, but *ex situ* and no reef edifice is known. This episode represents a shallowing with carbonate precipitation around three volcanic highs on Guam. The Miocene Bonya Limestone contains deeper-water facies with reef coral and coralline algae detritus but no reefs are preserved, so deposition was likely on a seaward slope between volcanic cones. The Miocene Alifan Limestone contains mudstones that grade to sparry packstones with well-preserved reef fauna and flora (*Porites*, *Acropora*, and *Halimeda*). The smallest limestone unit on Guam is the Tortinian and Pontian Janum Limestone consisting of deep fore-reef to basinal facies (Siegrist and Randall, 1992). The Mio/Pliocene Barrigada Limestone is a chalky foraminiferal-algal wackestone with some corals (*Porites*, and *Astraeopora*). While essentially all limestones show reefal fauna among their components, no Miocene reefs crop out in Guam or anywhere in the Mariana Islands (Siegrist and Randall, 1992).

The most widely distributed limestone is the Plio-Pleistocene Mariana Limestone, the dominant carbonate on Guam, Rota, Aguijan, Tinian, and Farallon de Medinilla (Siegrist and Randall, 1992; Randall, 1995) and also of great importance on Saipan. It contains well-developed reefal and peri-reefal facies. On Guam, it can reach a thickness of 175 m. Reef margin facies generally crop out as the most seaward facies and coincide often with the edges of terraces. Rocks are coralline and coralgal boundstones, coarse grainstones, packstones, and wackestones. Branching and massive corals occur *in situ* and in growth position and Siegrist and Randall (1992) report a rich fauna, reminiscent of the situation in modern reefs (*Acropora*, *Favia*, *Goniastrea*, *Leptoria*, *Platygyra*, *Pocillopora*, *Porites*, *Stylophora*, *Symphylia*, and *Turbinaria*). Detrital facies are common and contain benthic foraminifera, corals, mollusks, oysters, snails, and *Halimeda*. The Mariana Limestone has thoroughly altered porosity and mineralogy and displays many karst features (Siegrist and Randall, 1992).

Rota shares many rock units with Guam but is primarily (>90%) covered by carbonates, mainly Mariana

Limestone (Carruth, 2005; Figure 5). Near the shoreline, exposures of the Milencatan Limestone occur (Sugawara, 1934; Kayanne et al., 1993 refer to it as Milencatan while Bell and Siegrist (1988) refer to it as Mirakattan Limestone), which are an important sea-level indicator (Easton et al., 1978; Randall and Siegrist, 1988; Bell and Siegrist, 1988; Siegrist and Randall, 1992; Kayanne et al., 1993; Dickinson, 2000).

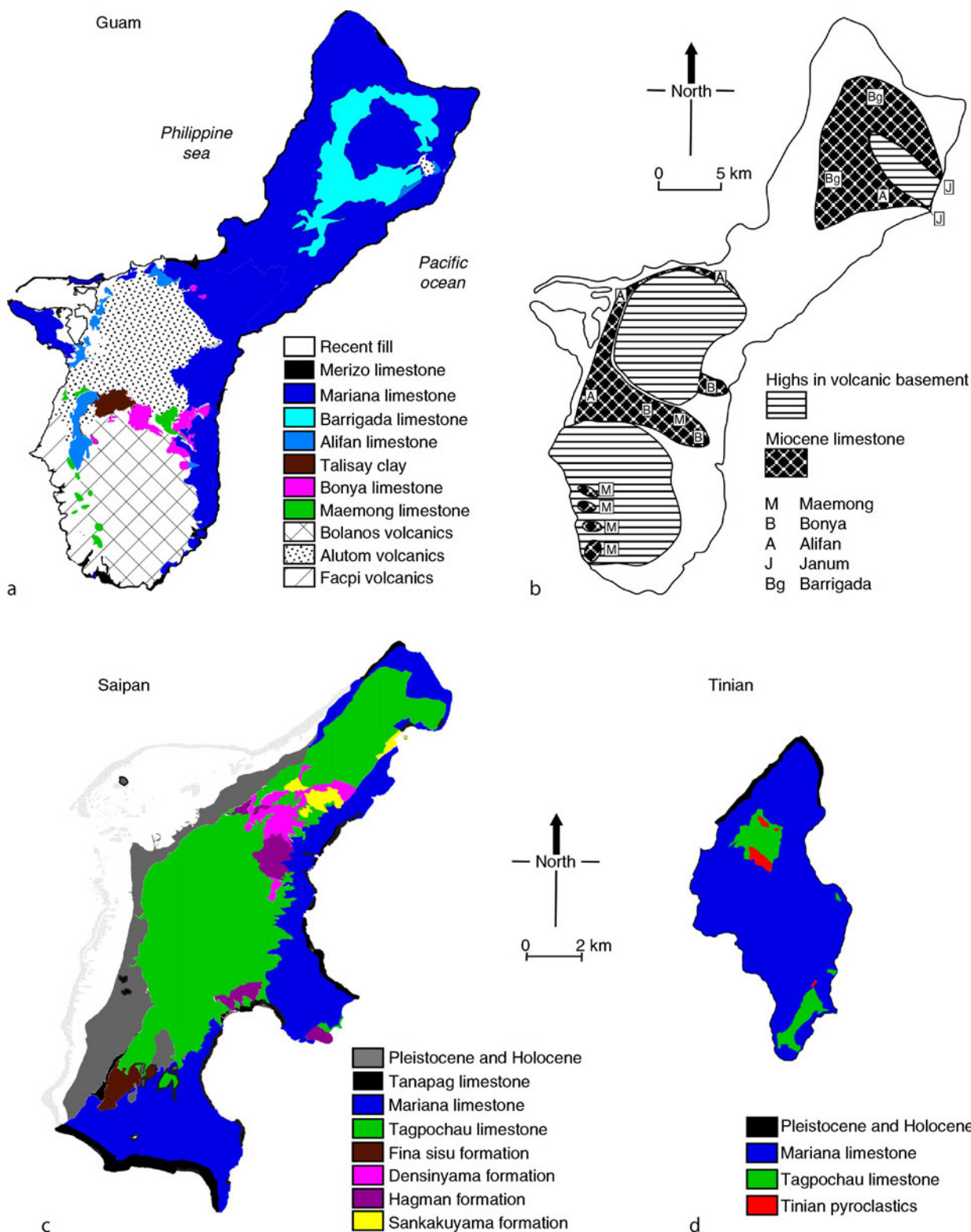
Saipan, the largest of the CNMI (48 sq. miles), consists of an andesitic-dacitic volcanic core (Sankakuyama Formation) overlain by sandstones, conglomerates, and breccias (Hagman, Desinyama, Fina Sisu Formations) which are capped by limestones covering about 95% of the island's surface (Figure 5). Volcanism on Saipan probably ceased in the Oligocene, after which marine deposition produced thick limestone sequences.

The Matansa Limestone is an upper Eocene carbonate bank deposit (Cloud et al., 1956). Saipan's center is covered by the early Miocene Tagpochau Limestone, a complex of calcareous clastic rocks. Saipan's eastern side is Pliocene Mariana Limestone, as found on Guam and Rota. It is reefal with argillaceous rubbly facies (Carruth, 2003) and differs from the Tagpochau Limestone in the abundance of corals and the modern aspect of its fossil assemblage. Mariana Limestone does not occur along the entire western coast but disappears under Tanapag lagoon (Figure 5). Thus, the structural control of the lagoon rim (= barrier reef) is probably determined by the course of the Mariana Limestone. Lagoon and the coastal lowlands seaward of the Tagpochau Limestone are probably fill, overlying the Mariana Limestone. The Tanapag Limestone is a Pleistocene to Holocene raised reef limestone, well indurated and porous with well-preserved coral heads and mollusk shells (Cloud et al., 1956). It formed as fringing reefs on an emerging surface with maximum thickness <20 m. Its younger, Holocene, parts are correlative to the Merizo Limestone of Guam and the Milencatan Limestone of Rota (Dickinson, 2000) and occur along the steep eastern shoreline of Saipan.

In Tinian, which is situated 5 km south of Saipan, the oldest rocks belong to the Eocene Tinian Pyroclastics (Doan et al., 1960), exposed in the central highlands and the island's southern section (Figure 5). The rest of Tinian is covered by limestones. The same Miocene Tagpochau Limestone as on Saipan is exposed on about 15% of the island. Pliocene Mariana Limestone covers the majority of Tinian (~80% of its surface and thickens from 0 to 150 m in all directions from near the Tinian Pyroclastics; Doan et al., 1960; Gingerich, 2002). Like on Saipan, the limestones on Tinian are heavily faulted and karstified. Recent alluvium and colluvium reaches thicknesses up to 13 m.

Farallon de Medinilla is the northernmost of the calcareous Marianas and is also mostly covered by Mariana Limestone (Randall, 1995). North of Farallon de Medinilla, the Mariana Islands bear no limestone caps and are volcanically active. This active island arc stretches from Anatahan to Uracas (Meijer and Reagan, 1981).





**Mariana Islands, Coral Reef Geology, Figure 5** (a) Surfacial geology of Guam (Modified from Gingerich [2002]). (b) Early Miocene volcanic highs in relation to Miocene carbonates show that the latter formed primarily as ramp facies on and around the volcanic cones (Siegrist and Randall, 1992). (c) Surfacial geology of Saipan (Modified after Carruth [2003]). (d) Surfacial geology of Tinian (Modified after Doan et al. [1960] and Gingerich [2002]).

## Conclusions

- Reef building in the Mariana Islands is confined to the inactive southern Arc from Guam to Farallon de Medinilla.
- The dominant coral reef type in the Marianas is fringing reefs, with barrier reefs only at Guam (Cocos Lagoon) and Saipan (Tanapag Lagoon).
- The northern Marianas are volcanically active and corals occur there, but tectonic instability and volcanic activity have precluded reef building.
- Reef building in the southern Marianas likely dates back to the Miocene, but no reef edifice has yet been found (corals and reefal fragments only).
- Late Holocene reef building in the southern Marianas is constrained by the presence of an early Holocene reef episode (Merizo Limestone on Guam, Milencattan Limestone on Rota, and younger part of Tanapag Limestone on Saipan) that clearly shows a mid-Holocene sea-level overshoot.

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## Cross-references

[Acanthaster planci](#)  
[Corals: Environmental Controls on Growth](#)  
[Earthquakes and Emergence or Submergence of Coral Reefs](#)  
[Emergent Reefs](#)  
[El Niño, La Niña, and ENSO](#)  
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## MASS EXTINCTIONS, ANOXIC EVENTS AND OCEAN ACIDIFICATION

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### Introduction

The five great mass extinction events that have greatly influenced paths of evolution of life on Earth have attracted a wide range of speculation about original causes and ultimate effects. In this context, reefs are among the most widely studied of marine communities, partly because carbonate platforms are so enduring, but also because the fossil record of corals is relatively well known in terms of abundance and distribution. The marine tropics in general and reef taxa have been particularly targeted in mass extinctions. In each case, they have taken many millions of years to recover, intervals of time known as “reef gaps.” Many authors have speculated on the causes of mass extinctions and reef gaps, the outcome being a wide array of hypotheses involving climatic upheavals of both terrestrial and extraterrestrial origin. This article reviews these proposals and examines them in the light of the biology of extant corals and their Pleistocene history.

### Mass extinctions, corals, and reef gaps

Mass extinction events are characterized by fundamental changes in plant and animal diversity as many high-level taxonomic groups go extinct over the same geological time interval. They are also characterized by very slow recovery, led by the evolution of new species rather than recolonization by survivors.

The five great mass extinction events occurred at widely spaced intervals, each at or near the end of major divisions in Earth history. Of these, extinctions at the Permian and Cretaceous were so profound that they respectively mark the end of the Palaeozoic and Mesozoic eras. However, present interest in mass extinctions is not so much in their geological timing, but in their cause, for they illustrate outcomes of extreme environmental upheavals and are thus worst-case scenarios of climate change.

Mass extinctions are usually perceived as dramatic catastrophes inflicted on an otherwise peaceful Earth, but this is

not the case. There were actually many minor or background extinction events at other times that left clear marks in the fossil record – no fewer than 27, according to a particularly detailed study (Raup and Sepkoski, 1986; Sepkoski, 1995). Although not global, some background extinctions were just as catastrophic as mass extinctions for particular ecosystems or particular places, and many had major impacts on coral reefs. Reefs, more than any other major type of ecosystem, leave a geological record that tracks such events (e.g., Sepkoski, 1995; Wood, 1999; Stanley, 2001). On an Earth history scale, this record does not show a process of gradual evolutionary development or improvement, but rather a stop-start response to a succession of environmental upheavals. Reefs are actually uncommon throughout the Phanerozoic and appear to have a “boom or bust” existence (Veron, 2008a and Kiessling, 2009). Environmental conditions that lead to reef proliferation are generally well understood; it is those which lead to their demise that are addressed below.

### The end Ordovician mass extinction

The first great mass extinction “event” took place at the end of the Ordovician, a time when, according to the fossil record, 26% of all families and 60% of all genera of both terrestrial and marine life worldwide were exterminated (Hallam and Wignall, 1997). This extinction occurred at the end of a period of high mean global temperatures, probably caused by global greenhouse stability, a condition that seems to have prevailed since the end of Cambrian 70 million years earlier. The extinction, however, was not just one “event.” It took place over a very long time span, perhaps several million years, and appears to have been the cumulative outcome of a succession of disasters. Possible causes that have been suggested include major fluctuations in sea level, multiple short-lived polar glaciations, and changes in ocean temperature, circulation, and chemistry. The extinction was particularly disastrous and long lasting for reefs (Webby, 1992; Copper, 2001). Extreme levels of carbon dioxide have been recently implicated (Berner, 2006). Although some individual rugose and tabulate coral taxa survived, living reefs disappeared from the face of the Earth and did not reappear for another 4–6 million years, long after the climate had returned to preextinction conditions. This is the first true “reef gap,” meaning a gap in the geological record of reefs.

### The late Devonian mass extinction

The Late Silurian to Late Devonian period – 75 million years or so of more or less global greenhouse conditions with high temperatures set between ice ages – probably included all-time peaks of Palaeozoic reef development (Copper, 2002). Sea levels were mostly high, so that seas flooded extensive areas of continents, forming epicontinental seas. However, despite the apparent proliferation of reefs, their development was intermittent, with major periods of worldwide expansion, especially during the



Middle Silurian to Late Devonian interspersed with periods of apparent collapse (Copper, 1994).

The world's Devonian reefs may have been every bit as well formed and biologically diverse as today's reefs and, with an estimated area of  $5 \times 10^6$  km<sup>2</sup> (including inter-reef areas), may have been as much as twice as extensive (Copper, 1994). The Late Devonian mass extinction, like that at the end of the Ordovician, has been linked to multiple causes. Many bolides may have struck the Earth around this time (McLaren and Goodfellow, 1990 and others), although this is unlikely to be linked to the extinction (reviewed by Racki, 2005). A precipitous drop in atmospheric carbon dioxide owing to uptake by vascular plants, low global temperatures, and wildly fluctuating sea levels have all been blamed (Copper, 2001). The extinctions appear to have varied geographically, although they primarily affected marine life: reef development ceased almost completely. Some corals and stromatoporoid sponges lived on, but there was no recovery for the vast coral-sponge reef-building communities anywhere in the world. Instead, the survivors were microbes. These continued to build carbonate structures, but these have none of the characteristics of "reef" or "coral reefs" built by skeleton-secreting organisms.

Reefs – although still not structures comparable to today's coral reefs – existed sporadically during much of the Carboniferous and Permian – through times of oscillating temperatures and sea levels, including the periodic development of polar ice caps. Some of these reefs, especially those of the Late Permian, were very extensive. Their fossil content indicates that they were exceptionally diverse relative to their forebears, for they contained extensive arrays of all of the major marine groups, especially molluscs, echinoderms, and crustaceans, as well as rugose and tabulate corals.

### The end Permian mass extinction

The fossil record of the end Permian mass extinction reveals a staggering loss of life: 82% of all genera and perhaps 80–95% of all marine species went extinct (Sepkowski, 1995, 2002; Erwin, 2006). All rugose and tabulate corals and most other calcifying organisms ceased to exist. The cause of this catastrophe was one of the foremost questions in palaeontology a century ago, and it remains so today. At one point or another, wildly fluctuating temperatures in response to sharp increases in atmospheric carbon dioxide, acid rain, and lack of oxygen in shallow waters after protracted times of plenty have all been held responsible. The oceans are widely believed to have turned anoxic and to have contained free hydrogen sulphide (Wood, 1999). Recent studies using biomarkers and isotopic data (Grice et al., 2005) are particularly revealing, one study suggesting that hydrogen sulphide generated by bacteria in deoxygenated oceans was so abundant that they released enough hydrogen sulphide to drive terrestrial extinctions (Ward, 2008). Other studies suggest that a sudden release of methane occurred at this

time (Ryskin, 2003; Erwin, 2006). Recently, a comprehensive palaeophysiological study clearly implicates carbon dioxide (Knoll et al., 2007), perhaps associated with the Siberian Traps, the biggest volcanic outpouring of all time. Whatever the cause (reviewed by Knoll et al., 2007), the impact on reefs was sudden by geological standards and devastating. Some members of most marine phyla survived, yet reefs did not reappear for about 10 million years, the greatest hiatus in reef building in all of Earth history. What emerged in the Middle Triassic was the Scleractinia in place of their Palaeozoic predecessors. There is much in common between the ancient reefs of the mid-Palaeozoic and the first scleractinian reefs that took their place, not so much in the animals that built them, but in the stop-start nature of their intervals of growth, their biodiversity, and the sheer size of the structures they formed.

### The end Triassic mass extinction

For 20 million years Triassic scleractinian corals, in concert with calcifying sponges and algae, went on to build some of the most spectacular reefs of all time. There was another substantial extinction of corals early in the Late Triassic, followed by a brief interval of dramatic recovery. Then, once again, the Earth plunged into a full-scale mass extinction. The end Triassic mass extinction (Stanley, 1988, 2001) – the fourth in the history of reefs – is estimated to have claimed about half of all marine invertebrates. The main taxa affected were conodonts (all), ammonites (almost all), and bivalves and gastropods (over half of all species). One-third of all scleractinian families went extinct and fewer than 25% of all genera are known to have survived (Beauvais, 1984). Nevertheless, this mass extinction, like its predecessors, was not only marine; perhaps 80% of all land quadrupeds also went extinct. The cause, again, has been much debated without a clear outcome (Wood, 1999; Flügel and Senowbari-Daryan, 2001). Atmospheric carbon dioxide reached extreme levels for the Mesozoic (perhaps eight times today's level) (Hautmann, 2004; Hautmann et al., 2008), and high greenhouse temperatures certainly resulted. Short-term sea-level fluctuations and various changes in ocean chemistry have been implicated by several palaeontologists, although none gives convincing evidence. The extinction was relatively abrupt (in geological time), making the reason for it particularly obscure. Whatever the cause, reefs again remained rare or absent throughout the world for a vast amount of time, perhaps 6–8 million years.

### The end Cretaceous mass extinction (K/T)

K/T has been extensively studied because of its indelible association with the demise of the dinosaurs. However, many well-known animal groups besides the dinosaurs went extinct at the K/T boundary. Virtually no large land animals survived. Plants were also greatly affected, although this is less clearly documented. Once again

tropical marine life was decimated, including a high proportion of calcifying organisms. All remaining ammonites and belemnites went extinct, as did a high percentage of bivalves, gastropods, and echinoids, as well as almost all Foraminifera. Many other unicellular organisms including radiolarians were also severely affected. However, most other major taxa – including freshwater fish, amphibians, turtles, crocodiles, snakes, and lizards – appear to have been almost unaffected, as were placental mammals.

Criteria used in extant coral taxonomy suggest that one-third of all families and 70% of all genera went completely extinct. Of the extant families, the Faviidae retained six of its original 16 genera; the others survived with only one or two. At least that is what the fossil record appears to say Veron (1995). However, that record is poor (Rosen and Turnšek, 1989; Kiessling, 2001) partly because sea levels were high during most of the Cretaceous and reefs were eroded away as the seas receded. Importantly, no branching corals appear to have survived, thus the habitats maintained by branching corals – those that provide shelter for algae-grazing fish – would have completely disappeared. On a taxonomic level, there are differences of opinion based primarily on what are considered to be valid records. Veron (1995) found that azooxanthellate corals were affected to the same degree as zooxanthellate corals, whereas Kiessling and Baron-Szabo (2004) on other criteria found that they were less affected. There are also differing views as to whether there was a reef gap or not. What is beyond dispute is that the fossil record is poor and few details been gleaned from it (Rosen, 2000).

Globally averaged atmospheric temperatures at the time of K/T have been estimated to be 6–14°C higher than at present (Barron, 1983), ranging from a few degrees' difference at the equator to as much as 20–40°C at the poles (Barron and Washington, 1985). Estimates of carbon dioxide levels vary greatly; however, the data for K/T are more reliable than those for more ancient extinctions. By the end Cretaceous carbon dioxide levels were at least five times, and perhaps as much as ten times, those of today (Berner, 1994; Tajika, 1999; Gale, 2000; Johnson et al., 2002).

A bolide hitting the Earth near the Yucatán Peninsula of southeast Mexico was widely thought to have caused the K/T extinctions (Alvarez et al., 1980). This theory, however, is highly controversial: over 2,000 books and articles were published about it within a decade of the original publication (Glen, 1990); the consensus now being that the bolide was not the primary cause of the extinction. The impact itself and the outpourings of the shock-induced volcanoes are widely believed to have created a stratospheric dust cloud that would have plunged the whole of the Earth into a cold, interminable night. Certainly acid rain (including nitric acid generated from heat-induced fusion of nitrogen and oxygen), high levels of carbon dioxide released from the impact site and from volcanic eruptions everywhere, and high concentrations of methane released from continental slopes would have combined to create intense greenhouse warming.

However, the timing of the ultimate extinction of different animal groups, the time taken for many to go extinct, and the age of the bolide debris do not correlate well. Some animal taxa became extinct within an apparently brief period, whereas others, including the dinosaurs, took hundreds of thousands of years, and their decline started long before the bolide's impact.

### Causes of mass extinctions

Extrapolations from today's knowledge of coral biology to past environments must be cautiously made, especially as the Scleractinia of today have been in existence for only two mass extinctions (the end Triassic and K/T). However, just as a number of physical parameters have remained effectively constant throughout the Phanerozoic, some physiological processes, while they may vary in detail over time, would in general have been applicable to the Scleractinia throughout their existence.

The causes of mass extinctions are divisible into two classes; those that do not involve the carbon cycle and those that do (Veron, 2008a, b).

### Causes independent of the carbon cycle

Reef development has three prerequisites: (1) corals (and/or other calcifying organisms) must exist in environments that are favorable for calcification, (2) the resulting calcium carbonate must be consolidated into reefs, and (3) the rate of erosion must be less than the rate of accretion. Mass extinctions and reef gaps might occur whenever calcification is decreased, or there is a breakdown in the mechanisms of consolidation, or there are factors that increase the erosion or dissolution of calcium carbonate. In the case of K/T, where there was a simultaneous extinction of both zooxanthellate and azooxanthellate coral species, any explanation of extinction must span wide depth ranges as well as broad spatial scales.

#### *Direct physical destruction from bolides*

A bolide many kilometers across could possibly cause massive destruction of reefs along the exposed side of an area the size of a continent; however, it beggars belief that such an effect, from a single point source, could envelop the whole Earth (Toon et al., 1997). Nor is there any way that azooxanthellate species would be equally affected or that surviving reef corals would take millions of years to recommence reef building. Be that as it may, the Earth has several large and well-known craters (13 of which date to the early Mesozoic or later) (Jablonski, 1986), and many studies, motivated by the discovery of the K/T bolide, have sought to establish these as the primary cause of extinction events. Yet credible links have not emerged (Rothschild and Lister, 2003). Indirect effects of bolides are another matter.

#### *"Nuclear Winter" induced by dust clouds*

Bolides are presumably capable of creating dust clouds that may have enveloped the Earth for weeks or months, creating devastating darkness and (for terrestrial life) cold.

Survival estimates for corals under conditions of very low light vary from death in just a few weeks to survival of at least parts of colonies for six months or more. Significantly, this strongly suggests that, if today's reef-building species were suddenly subjected to conditions of very low light for periods of years rather than weeks or months, 99% of species would go extinct. No such extinction has ever happened to the Scleractinia. The proportion of zooxanthellate corals that went extinct at K/T is not on its own sufficient to explain the end of reef building or the reef gap that followed: (1) Many taxa that survived, including members of the Poritidae and Faviidae, are among the best reef builders (Veron, 1995). (2) Azooxanthellate taxa fared no better than zooxanthellate taxa. (3) The K/T mass extinction caused a much higher rate of extinction in corals than in many other photosynthetic organisms, notably terrestrial vascular plants, which would have been more vulnerable to prolonged darkness.

From a biological point of view, it can be concluded that very low light, even if maintained for months, is exceedingly unlikely to have been the principal cause of the K/T mass extinction event. The dust cloud created by the K/T bolide would also have caused atmospheric temperatures to plunge, but only for as long as the cloud persisted. The thermal inertia of the oceans would have protected marine environments from significant temperature change.

#### *Sea-level changes*

The major sea-level changes throughout Earth's history have been due to plate tectonics. These are very different from the sea-level changes that occurred during the Pleistocene, primarily in being much slower and of immensely longer duration. During the last glacial cycle, the sea level dropped 130 m (Lambeck and Chappell, 2001; Siddall et al., 2003). This fall is more than the depth range of all but a few deepwater zooxanthellate corals, which means that almost all corals had to relocate. Throughout the Pleistocene, such falls were repeated many times, yet only about 10% of all corals went extinct over this entire interval (Veron and Kelly, 1988). This is no more than a background extinction rate. Thus sea-level changes of any kind, let alone those resulting from tectonic movements, can be discounted as a primary cause of coral species extinctions.

#### *Loss of area during sea-level regression*

Loss of reef area during sea-level changes of the past has been suggested as a cause of coral extinctions, but the Pleistocene history of modern corals offers a number of reasons why this would not be so. There were major losses of reef area during the last glacial cycles; however, these had no significant effect on today's coral diversity. At the opposite extreme, small areas may have most of the species complement of an entire province. The great dispersal capabilities of corals would ensure that recolonization would take place swiftly from surviving niches. Area loss is thus highly unlikely to have been a primary cause of any

extinction. Furthermore, azooxanthellate species would have been unaffected by a loss of reef area.

#### *Loss of biodiversity as a cause of reef gaps*

Reef building does not depend on high species diversity. Many of the corals that survived K/T belonged to genera well able to build reefs in the absence of any other coral species. We can therefore discount loss of biodiversity as a primary cause of reef gaps.

It has also been suggested that reefs do not reestablish until peak evolution rates of new species are reached (Jablonski, 1986). Although this may have been true after some mass extinctions (there is no evidence either way), it was certainly not the case after K/T as coral diversity remained low long after widespread reef building had reestablished.

#### *Low temperatures*

Conceptually, low temperatures could explain reef gaps and coral extinctions, but the data available for global temperatures give no credence to this. During the K/T extinction, ocean temperatures were at or above, rather than below, present levels. Furthermore, the suite of reef-building genera that survived indicates no selection for cold tolerance. Nor does low temperature explain why azooxanthellate species were lost. Even during a full glacial cycle, the world's oceans cool only around 6°C, and less than this at the equator. Although temperature reductions of this extent would be enough to contract the latitudinal range of species today, such a decrease could not have initiated extinctions in equatorial regions on the scale of any mass extinction.

#### *High temperatures*

Elevated temperatures can cause mass bleaching of corals, creating widespread devastation when reef ecosystems become so degraded that they are taken over by macroalgae and bacterial slime. However, mass bleaching only occurs in zooxanthellate organisms as it is due to an overproduction of photosynthetic oxygen. Over geological time, corals growing under such conditions have the evolutionary option of avoiding the issue by becoming azooxanthellate. In such circumstances, any reduced capacity for calcification would be in part offset by the effects of temperature. Furthermore, a mass extinction from temperature would require that such temperatures extend to highest latitudes. This would never have been possible, even under the most extreme conditions. High temperatures cannot explain the extent or global nature of mass extinction events, nor can they account for the species that survived K/T, nor the loss of azooxanthellate taxa.

#### *Salinity*

Corals, and by extension reefs, are adversely affected by low salinity and low salinity may well have been a major cause of regional extinctions at various times, especially in partly landlocked regions such as the epicontinental



seas of the Super-Tethys and North Africa during the Cretaceous. However, it is inconceivable that any continental landmass could hold enough fresh water to cause a global mass extinction.

#### *Disease and toxins*

There is strong evidence today that stresses such as mass bleaching, hyposaline influxes, and a wide range of other ecological imbalances can greatly increase the incidence of diseases in corals. Combinations of stresses from high temperature, high light levels, and disease might lead to major regional losses of corals for as long as those stresses persist. These would have to be very widespread and affect deepwater and nearshore corals equally. The Earth has no toxins in such quantities, nor any that can exist both on land and in the oceans.

#### *Extraterrestrial events*

Extraterrestrial events apart from bolides have commonly been suggested as causal factors in extinctions. Episodes of ultraviolet or cosmic radiation from solar flares or supernovas (which may be capable of stripping away the ozone layer, allowing high levels of ultraviolet radiation to reach terrestrial life) can be discounted as causes of mass extinctions because the deep ocean would have shielded bottom-dwelling communities, and these were not shielded. There is also the often-mentioned finding that extinctions follow a 26-million-year periodicity, implying an overriding extraterrestrial “supercycle” of unknown origin. The database of fossils referred to above presents an avalanche of statistics in support of this conclusion (Raup and Sepkoski, 1986); nevertheless, although this long periodicity does not look entirely random, it does not look distinctly cyclical either, so this concept remains enigmatic and without a plausible mechanism.

#### **Links between mass extinctions and the carbon cycle**

If the above causes of mass extinctions and reef gaps are discounted as primary factors, there remains an array of further possibilities that have one aspect in common: they are either part of the carbon cycle or closely linked to it. This is hardly surprising, for of all the great matter cycles of the Earth, the carbon cycle is by far the most important.

The chemical impacts discussed below are all directly or indirectly linked to the carbon cycle. Severe environmental degradation can occur rapidly in response to bolide impacts and some geological events such as larva flows (traps) or supervolcanoes. They may also occur in response to slower processes created by gases release from volcanic chains as a result of seafloor spreading and other tectonic movements. Although slow, these processes may lead to relatively abrupt extinctions through cumulative outcomes and synergies.

Importantly, small changes in the concentration of atmospheric gases can lead to major changes in global environments, potentially affecting both marine and terrestrial life. These gases include major components of

our atmosphere, notably oxygen and water vapor, as well as those that are only present in trace amounts. The latter include the gases that control the atmosphere's greenhouse warming of which carbon dioxide and methane being the most important.

Peripheral links to the carbon cycle are considered here first.

#### *Acid rain*

High levels of atmospheric carbon dioxide produce carbonic acid, and high levels of sulphur dioxide produce sulphuric acid. These substances, together with nitrous oxide from industry and the draining of tropical marshlands, are the main sources of acid rain today. Carbon dioxide and sulphur dioxide are released in massive amounts from some volcanoes, traps (notably the Deccan Traps of India at the time of K/T) and other sources, both terrestrial and marine, both to be ultimately neutralized by ocean buffers. Although sulphur dioxide and nitrous oxide do not contain carbon, by the time their products reach the oceans they do, and thus they are inextricably linked to the carbon cycle. It is not quantitatively possible for acid rain to be a primary cause of an extinction event; however, acid rain may well have acted in synergy with other causes to create extreme environmental degradation.

#### *Hydrogen sulphide*

Hydrogen sulphide is another gas released in large quantities into the oceans and atmosphere from volcanoes or from sulphur-rich geysers and the like. It also has biological origins, which is why it regularly occurs in anoxic waters of all types, ranging from aquaria to atoll lagoons. As with sulphur dioxide, although it does not contain carbon, it is inextricably linked to the carbon cycle and could, in terms of quantity, have been a significant contributor to an environmental upheaval in synergy with other gases.

#### *Oxygen and anoxia*

In a nitrogen-dominated atmosphere, oxygen and carbon dioxide have an additive relationship, an increase or decrease of the one creating a parallel effect in the other, all else being equal. However, all else may sometimes not be equal, and there may have been conditions, perhaps the end Permian and K/T, where ocean anoxia may have been created by primary productivity decrease (through phytoplankton depletion) as a result of acidification. By this simple mechanism, high levels of atmospheric carbon dioxide can work synergistically with low levels of atmospheric oxygen to create ocean anoxia. Whether or not this has actually happened is not known.

#### *Methane*

Methane from geological sources, plant respiration, and some animal life exists in minute amounts in the atmosphere (currently 1.8 ppm). However, it occurs in much greater quantities in permafrost, in tropical marshlands, and in vast quantities as icelike solids (clathrates or hydrates) that are stable only under pressure and at low

temperatures on continental shelves. The volume of these solids is unknown, although it is of the same order of magnitude as the Earth's total quantity of fossil fuels. Methane leaks into the ocean and atmosphere naturally, for example, as marsh gas. However, if it were released into the atmosphere in substantial quantities, perhaps as a result of a bolide impact or a buoyancy change in the methane ice (for which there are many possible causes), there could be serious environmental consequences. It would have a major greenhouse effect (methane has 22 times the potency of an equal volume of carbon dioxide) and would also be converted to carbon dioxide by microbes and chemical oxidation, causing the same adverse effects characteristic of high levels of carbon dioxide.

#### *Carbon dioxide*

Both increasing and decreasing carbon dioxide levels have been proposed as major contributors to mass extinction events in the past. Over geological time scales, carbon dioxide has varied from levels much lower than the 387 ppm of today up to perhaps ten times today's level (depending on the reliability of studies of a small number of fossil soils and whether or not results from single points in time are representative of longer time intervals). The effects of high levels of atmospheric carbon dioxide are pursued below.

#### *Ocean chemistry and pH*

This subject can only reliably be assessed via the chemistry of contemporary oceans. Increased atmospheric carbon dioxide leads to greater amounts of the gas dissolving in the oceans, which directly reduces pH. This, in turn, alters the proportions of different forms of inorganic carbon ( $\text{CO}_2$ ,  $\text{H}_2\text{CO}_3$ ,  $\text{HCO}_3^-$ , and  $\text{CO}_3^{2-}$ ) in the ocean (Buddemeier et al., 2004; Kleypas and Langdon, 2006). Increasing the concentration of carbon dioxide in the ocean alters the proportion of the other three forms of carbon. Calcifying organisms use carbonate and/or bicarbonate ions to build skeletons, and thus a decrease in their availability slows the calcification process. The proportions of each of these carbon components are sensitive to temperature and pressure, and thus to latitude and depth.

Acidification affects zooxanthellate corals and most azooxanthellate corals by different paths. The former are sensitive to acidification of surface waters by atmospheric carbon dioxide directly; the latter are sensitive to having their depth range reduced by shallowing of  $\Omega_{\text{aragonite}}$ . These surface and deep layers directly influence each other at high latitudes where temperature gradients are weak and mixing occurs relatively easily. However, they are well separated in the warm tropics, especially at the thermocline, and interact primarily via the sinking of carbonate skeletons of surface-dwelling plankton.

Shallow oceans are currently supersaturated with carbonates, allowing zooxanthellate corals to calcify. However, as  $\Omega_{\text{aragonite}}$  decreases, calcification requires increasing amounts of energy. The same applies to azooxanthellate corals, although here the process depends

on the depth of the aragonite saturation horizon, which, in turn, varies with temperature as well as chemistry: as changes in water temperature and chemistry cause the horizon to rise, the depth range of azooxanthellate corals shallows.

#### *Acidification*

The dependence of calcareous algae on high-magnesium calcite, the most soluble of all calcium carbonate skeletons, makes them particularly vulnerable to acidification (Kiessling et al. 2008, Veron, 2008b). Since these algae are critical to reef consolidation, their removal would, in the past, reduce the net accretion of reefs before the rate of coral calcification became limiting. With further decrease in pH, aragonitic organisms including Scleractinia would become increasingly affected, further tipping the balance in favor of reef erosion. Since acidification from elevated atmospheric carbon dioxide affects oceans on a global scale, the effects on reefs would be worldwide, although influences from temperature and surface water mixing would create local variations both geographically and with depth. In equatorial regions, adverse changes in carbonate/bicarbonate ion availability as a result of decreasing pH would be exacerbated by lack of mixing between the warm, shallow, carbon dioxide-enhanced surface layers, and the buffers of cool, deeper ocean water. Acidification could thus have a devastating effect on reef development, leading initially to widespread inhibition of reef growth and eventually to reef erosion and dissolution.

The first impact will be on azooxanthellate taxa, which would be to displace them from deeper oceans as the  $\Omega_{\text{aragonite}}$  horizon shallows. This effect is greatest at high latitudes (Guinotte et al., 2003; Turley et al., 2007). Two recent studies point toward acidification as the primary cause of coral extinctions and the reef gaps, despite deficiencies in the fossil record. (1) Late Cretaceous azooxanthellate corals of the caryophylliid genus *Coelosmia* have been found to have calcitic skeletons rather than skeletons of the more soluble aragonite as have today's Scleractinia (Stolarski et al., 2007). (2) Two Mediterranean corals, *Oculina patagonica* and *Madracis pharensis* which were placed in acidified aquaria gradually lost their skeletons, then regrew them after being returned to normal seawater (Fine and Tchernov, 2007).

Unlike the alternative causes of extinctions noted above, acidification can explain why both azooxanthellate and zooxanthellate species were affected at the time of K/T. It can also explain the loss of reefs both locally and globally, as well as account for the existence of long-lasting reef gaps. Although acidification may be difficult to initiate because of ocean buffers, once achieved it will persist as long as atmospheric carbon dioxide remains high. Furthermore, the oceans would remain acidified for tens of thousand years after carbon dioxide levels had declined, that being the time required for normal alkalinity to be restored. This would be an interval long enough for corals to initiate an evolutionary recovery. Under such

a recovery sequence, reef gaps in the past of millions of years would be a plausible consequence, depending primarily on the endurance of atmospheric carbon dioxide and the rate of evolutionary accommodation to it.

#### *Low levels of carbon dioxide*

Low levels of carbon dioxide may result in low levels of photosynthesis, leading to low levels of oxygen and eventually ocean anoxia. This might have triggered the Late Devonian mass extinction event; the evidence is inconclusive.

### Conclusions

The foregoing discussion argues that ocean acidification and anoxia as a mechanism explains mass extinctions better than other mechanisms that have been offered. However, studies of ancient environments also suggest that similar atmospheric carbon dioxide levels may have occurred at times when reefs actually proliferated rather than declined. One explanation may lie in the interpretation of information from ancient times for carbon dioxide data are very uncertain for most of geological time as it is based on a small number of point samples from widely different geological intervals. In contrast, as seen in ice core records and contemporary measurements, carbon dioxide levels can fluctuate substantially over intervals as short as millennia. Many possibilities present themselves. (1) Reefs may not have proliferated at all during carbon dioxide highs; they only appear to have survived because they were able to resume growth when levels fell (the boom or bust observation made above). (2) The high apparent carbon dioxide levels of ancient times may be an artifact of a lack of data and measuring methods, which currently produce very conflicting results. (3) Corals and other taxa may have become partly or completely askeletal (as noted above) during times of adverse ocean chemistry. (4) Corals may have had calcitic skeletons during such times and the calcifying process may have been more physiologically isolated from ocean pH than it now is. These options can only be guessed; there may have been many aspects of coral biology that allowed ancient corals to tolerate water chemistries that are lethal to today's taxa.

Although these deliberations about possible causes of mass extinction events have highlighted acidification as the most probable cause of both coral extinctions and reef gaps, it would be misleading to consider this as the only cause. Indeed, all mass extinctions appear to be the outcome of several different influences acting synergistically. Acidification may well have been a primary mechanism by which marine ecosystems were affected; however, low light, bleaching, deteriorating water quality owing to acid rain or anoxia, mechanical damage, and disease would all have played their parts. Although the time frames of bolides do not always fit the facts as a singular cause of extinction, bolides or traps or volcanic chains may have created severely adverse conditions that became "the straw that broke the camel's back."

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## Cross-references

[Aragonite](#)  
[Carbon Fluxes of Coral Reefs](#)  
[General Evolution of Carbonate Reefs](#)  
[Ocean Acidification, Effects on Calcification](#)  
[Scleractinia, Evolution and Taxonomy](#)

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## MAYOR, ALFRED GOLDSBOROUGH (1868–1922)

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Born in Frederick, Maryland, on 16 April 1868, Alfred Goldsborough Mayer (spelling changed to Mayor in 1918) was the son of Alfred Marshall Mayer, a noted American physicist. Although an excellent student of mathematics and physics, young Alfred preferred zoology as his field of study. However, as his strong-minded father wanted his son to pursue a career in the physical sciences, Alfred majored in engineering at the Stevens Institute of Technology, in Hoboken, New Jersey, from which he graduated in 1889. He began advanced work in physics soon thereafter, but decided to enter the graduate program in zoology at Harvard University in 1892, where he came to the attention of Alexander Agassiz, a prominent marine zoologist and director of Harvard's Museum of Comparative Zoology (MCZ). Agassiz soon placed Mayor in charge of the MCZ's division of coelenterates and other radiate species.

Mayor collected specimens for the MCZ in various locations on the east coast of America and around the Dry Tortugas, in the Gulf of Mexico. Between 1896 and 1900, he also accompanied Agassiz on three major collecting expeditions in the South Pacific Ocean. Mayor received the Ph.D. degree in 1896, but continued in his position at the MCZ until 1900, when he left to become curator of zoology in the Brooklyn Museum.

In 1903, the Carnegie Institution of Washington (CIW) approved Mayor's proposal for establishing a tropical marine laboratory on Loggerhead Key, in the Dry Tortugas, and made him director of the new station, which opened in 1904. During the early years of the Laboratory, Mayor worked mainly on jellyfish taxonomy, and, in 1910, completed the monumental three-volume work titled *Medusae of the World*. Two years later, he published *Ctenophores of the Atlantic Coast of North Atlantic*, a standard work on the comb jellies.

Influenced by the studies of the prodigious coral geologist Thomas Wayland Vaughan, who conducted considerable research at the Tortugas Laboratory, Mayor began around 1913 to focus his attention on the stony corals. In the waters of the Florida Keys and later those of the South Pacific, Mayor concentrated on the ecology of coral reefs, and produced a number of pioneering studies on the growth-rate of corals and the effects of temperature, light, water depth, wave action, fresh water, and silt on coral development. In 1917, he began to use a diving helmet to further his studies, thus becoming one of the first biologists to conduct underwater explorations of reefs. Mayor was elected to membership in the National Academy of Sciences in 1916.

By the time of his premature death on 24 June 1922, on Loggerhead Key, Mayor had achieved international acclaim for his pioneering work in jellyfish and comb jelly taxonomy and on coral-reef ecology. A monument in his memory was erected on Loggerhead Key in 1923.

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## Cross-references

Agassiz, Alexander (1835–1910),  
Vaughan, Thomas Wayland (1870–1952)

## MEGABLOCKS

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## Synonyms

Boulder or megaboulder deposits; Coral boulders; Coral megablocks; Erratic coral boulders

## Definition

*Megablocks*. Intact blocks or boulders, often composed of coral and occasionally with dimensions of 10 m or greater, situated well apart from (as much as 100–500 m) and sometimes well above (up to 30 m) their original formation sites.

## Introduction

Coral megablocks are large erratic boulders detached from the reefs or paleoreefs where they formed, and presently situated in the surf zone, along the beach, or still further inland. We distinguish megablocks from sea stacks, which are coral formations that may be similar in size and location to megablocks but are still in growth position, attached at their bases. Megablocks as discussed here are also distinct from tectonic segments or arc segments, often described along subduction zones, which are tectonic blocks with horizontal dimensions up to tens of km or greater that undergo coherent lateral or vertical motions distinct from the motions of adjacent blocks or segments. There is also a vast literature describing ice-raftered or glacier-deposited boulders composed of materials other than coral; for example, glacier-transported boulders reported in Tierra del Fuego by Charles Darwin (1842) are still being studied today (Kaplan et al., 2007).

Scientific interest in megablocks, whether composed of coral or otherwise, often focuses on determining the mechanism and timing of their emplacement. Where coral megablocks may have been emplaced by prehistoric storms or tsunami waves, analysis can provide information about potential hazards from natural events too rare to be represented in the historical record.

## Examples

Erratic megablocks often occur near and below sea cliffs. Although the specific mechanism of transport may be uncertain, in most cases a plausible explanation is that the blocks separated from the cliff due to the action of surf, biological activity, earthquakes, or weathering, and subsequently were transported downhill via mass wasting.

However, coral megablocks also occur where sea cliffs are absent, and may lie well above their original sites of formation (Scheffers and Kelletat, 2003). To emplace these, storm or tsunami waves are the most credible mechanism (e.g., Zhao et al., 2009), especially as some such emplacements have occurred historically. The 26 December 2004 Indonesian tsunami deposited hundreds of meter-sized coral boulders in the intertidal zone along Pakarang Cape, Thailand (Goto et al., 2007), including some with estimated weights up to 40 tons (Kelletat et al., 2007). On 27 August 1883 the island of Krakatau in Indonesia experienced a huge explosive eruption; at Anyer beach at a distance of 40 km, this produced a tsunami with a reported height of 36 m that moved coral megablocks distances up to 240 m. The largest transported megablock had a reported volume 317 m<sup>3</sup> and an estimated mass of 600 tons (see picture in Simkin and Fiske, 1983).

A third well-studied historical example of megablock emplacement is on the island of Ishigaki, in the Okinawa group, offshore Japan. Here in April 1771, a tsunami accompanying an earthquake killed some 12,000 island residents and also displaced numerous coral boulders, some with dimension  $\sim 5$  m (Imamura et al., 2008). Controversies surrounding this incident concern (1) whether an earthquake rupture on any regional fault was alone sufficient to generate the tsunami, or whether the earthquake triggered an undersea landslide (Nakamura, 2006); (2) the height of the tsunami, variously reported as 30–85 m, and the geographic extent of its runup; and (3) whether the 1771 tsunami alone emplaced the megablocks, or instead they were emplaced by previous storms or tsunamis and simply moved again in 1771 (Suzuki et al., 2008).

There are no historical records of emplacement for many megablocks. Frohlich et al. (2009) studied coral megaboulders along the western coastline of Tongatapu in the southwest Pacific. The largest stone (see Figure 1) is situated  $\sim 10$  m above present sea level and 130 m from the present shoreline. It is one of seven similar megablocks found along a 3-km arc 100–400 m from the present shoreline. The blocks contain well-preserved corals demonstrating that the stones are no longer in growth position. All these stones are the highest features locally. Frohlich et al. (2009) concluded that these megablocks were emplaced by a tsunami, generated probably by explosive volcanism along the Tofua arc  $\sim 30$  km west of Tongatapu, or possibly by an undersea landslide just offshore. Other examples of

exceptionally large coral megablocks occur in the Bahamas (Hearty, 1997), and in the Tuomotu Islands (Bourrouilh-Le Jan and Talandier, 1985).

### Origin and mechanism of transport: Tsunamis or storms?

In coastal environments, elucidating the circumstances of megablock emplacement provides crucial information about rare but very severe natural hazards, especially as the historical record in many locations covers only the past century or two. However, there is often controversy about whether storms or tsunamis emplaced the megablocks (e.g., Nott, 2004). This is partly because historically documented storms have displaced some rather large boulders, and partly because distinguishing the characteristics of tsunami-emplaced vs storm-emplaced deposits is a still-developing field (Morton et al., 2007). For example, Noormets et al., (2002) describe a 96 ton megablock emplaced by the 1946 tsunami and since twice moved by storm waves on Oahu in Hawaii.

The largest historically documented storm-emplaced stones displaced vertically upward and moved distances exceeding a few meters have average dimensions smaller than  $\sim 5$  m and masses less than 100 tons (Nott, 2004); we conclude that larger megablocks are probably tsunami-emplaced as it is likely that the historical record includes storms having near-maximum possible intensities. Wind speeds, wave heights, and storm surge characteristics correlate roughly with the diameter of the



**Megablocks, Figure 1** A large coral megablock on the island of Tongatapu, southwest Pacific. This block has dimensions of  $15 \text{ m} \times 11 \text{ m} \times 9 \text{ m}$  and sits with its base 10 m above sea level and  $\sim 130$  m from the present shoreline; it is one of seven megablocks that form a group on western Tongatapu.



storm's circulation pattern, and the historical record includes storms such as 1979 typhoon Tip in the western Pacific which had a diameter of 2,200 km (Dunnavan and Diercks, 1980). This is larger than the Gulf of Mexico, the Caribbean, or the Mediterranean; it is difficult to imagine sustaining a significantly larger storm. There has been discussion that sea surface temperatures exceeding 36°C might generate 'hypercanes', storms much stronger than any observed historically (Parks Camp and Montgomery, 2001). However, no one has yet suggested that such conditions occurred within the past several million years.

Tsunamis may be generated by several different natural phenomena, including earthquakes, undersea landslides, subaerial landslides that reach the sea, undersea volcanic eruptions or flank collapses, and meteoroid impacts. Although tsunami hazard analyses focus principally on earthquake-induced tsunamis, the largest tsunami waves are generated by other causes. For example, two of the highest historical tsunami waves were generated by a subaerial landslide (wave runup to 520 m elevation, Lituya Bay, Alaska, 1958; see Mader and Gittings, 2002) and a volcanic eruption (~36 m waves, Krakatau, Indonesia, 1883; see Simkin and Fiske, 1983).

Evaluating megablock occurrence may help quantify hazards and occurrence rates for undersea landslides. This is important because several investigations conclude that giant-to-moderate (100–10 km<sup>3</sup>) submarine slope failures may cause exceptionally large tsunamis (Ward and Day, 2001). Sometimes undersea landslides accompany or are triggered by earthquakes and produce tsunamis much larger and more devastating than those attributable to the earthquake alone (e.g., the 18 November 1929 Grand Banks earthquake; see Fine et al., 2005; and the 17 July 1998 New Guinea earthquake; see Heinrich et al., 2001; Satake and Tanioka, 2003). In many coastal locations even a cursory evaluation of offshore bathymetry demonstrates that undersea landslides have occurred.

### Dating the emplacement of megablocks

During the past 400 ky, sea level has only been at or above its present only during interglacials. Interglacial highstands typically occur at intervals of about 100,000 years and have durations of ~10,000 years. The two most recent highstands are the past 7,000 years and 120–130 ka; thus these are the most plausible times of emplacement for large megablocks presently situated at elevations near or above their sources. Generally the more recent interval is likely because exposed coral limestone dissolves with rainfall, destroying megablocks over time. During subsequent highstands, sea level returns to near the level of paleomegablocks and they are destroyed by bioerosion. And of course, any that were deposited during lower sea levels are now underwater or had sea level pass over them, thereby eroding them and then burying them under new reef growth. When megablocks contain well-preserved corals, <sup>230</sup>Th dating can determine when they

lived and thus constrain an earliest credible time for emplacement.

Where megablocks occur as part of a well-preserved stratigraphic sequence emplaced by a storm or tsunami, this may contain mineral or organic material datable using U-series or <sup>14</sup>C methods. Where megablocks contain identifiable coral species indicating that the blocks are overturned, it may be possible to use <sup>10</sup>Be or <sup>26</sup>Al to estimate how long the upper surface has been exposed (e. g., see Nishizumi et al., 1993).

In some environments where erratic megablocks are situated on a raised coral-reef terrace, they are perched on pedestals that have formed beneath the blocks as the adjacent terrace limestone is dissolved by rainfall solution. Matsukura et al. (2007) describe examples of such perched megablocks found on Kikaijima Island in the Ryukyus; they estimate that the dissolution rate of the unsheltered terrace surface is ~205 mm/ky. As many pedestal heights are ~1.0–1.5 m, they conclude that the megablocks were deposited on a reef flat which emerged and began experiencing dissolution about 6,000 years ago. Although it might seem that measuring pedestal heights would provide an accurate way of dating megablock emplacement, at present this is a subject for additional research as reported dissolution rates vary by two orders of magnitude or more and depend on numerous factors including amount of rainfall, whether or not the block is exposed to both rainfall and sea spray, average temperature, and porosity and composition of the terrace surface.

### How fast the current? How high the wave?

Wherever large erratic megablocks occur, they provoke the question of how strong a current was required to displace them. If they are situated on land, how high was the storm or tsunami wave that moved them?

A physics-based analysis provides some approximate answers to these questions. In classical hydrodynamics, an object of cross sectional area  $A$  in a fluid of density  $\rho_w$  streaming at velocity  $V$  experiences a drag force of  $\frac{1}{2}C_d\rho_wAV^2$ , where  $C_d$  is a dimensionless parameter known as the drag coefficient which is ~1/2 for objects such as smooth spheres. To displace a megablock with dimension  $h_b$  and density  $\rho_b$ , the drag force approximately equals its buoyant weight; thus as its cross section is  $\sim h_b^2$  and its volume is  $\sim h_b^3$ ,

$$\frac{1}{2}C_d\rho_w h_b^2 V^2 > g(\rho_b - \rho_w)h_b^3 \quad (1)$$

and

$$V > \sqrt{\frac{2g}{C_d} \left( \frac{\rho_b}{\rho_w} - 1 \right) h_b} \quad (2)$$

If a wave impacts a shoreline, potential energy stored at the wave crest may be converted to kinetic energy, producing a current as the wave breaks and flows onshore. Estimating the height  $h_w$  of the wave necessary to displace

a boulder depends on various assumptions about the dimensions and hydrodynamic properties of the boulder (e. g., see Nott and Bryant, 2003; Noormets et al., 2004). However, a very crude ‘rule of thumb’ is that

$$h_w > \frac{\rho_b}{\rho_w} h_b; \quad (3)$$

i.e., the height of a wave necessary to displace a boulder of given density and height is approximately proportional to the product of the boulder’s relative density and its linear dimension. This is often an adequate estimate as generally knowledge of the boulder’s hydrodynamic parameters and density  $\rho_b$  (see Spiske et al., 2008) is highly uncertain.

In practice, the interaction of waves and shorelines is highly nonlinear and depends critically on details of the nearshore bathymetry, and thus computer modeling is required to obtain substantially more accurate results (Mader, 2004). Of practical importance is the observation that boulders entrained in a tsunami tend to saltate, tumbling end-over-end rather than sliding, and thus attention to the dimensions and orientations of megablocks may provide information about the direction of the flow that emplaced them (Imamura et al., 2008).

## Summary

Megablocks are erratic coral boulders, some with dimensions as great as 10 m or more, found in and landward of active reef zones. In locations where they can only have been wave-emplaced, they provide important information about the frequency and intensity of rare, very large storms and tsunamis. However, at present identifying the specific characteristics that constrain the features of the waves that emplaced them, or that confirm their origin to be a storm or tsunami, is still a subject of active research.

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## Cross-references

[Boulder Beaches](#)  
[Earthquakes and Emergence or Submergence of Coral Reefs](#)  
[Last Interglacial and Reef Development](#)  
[Recent Sea Level Trends](#)  
[Tsunami](#)

## MELTWATER PULSES

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## Synonyms

[Catastrophic \[sea-level\] rise event](#); [Sea-level jump](#)

## Definition

A meltwater pulse is an acceleration in sea-level rise which results from outbursts of pro- or subglacial meltwater and/or surging of ice-streams into the ocean during ice-sheet disintegration. Radiometric ages of coral-reef drowning and back-stepping indicate that rates of sea-level rise during these meltwater pulses were at least 35 mm/yr and may have been as much as 60 mm/yr, and that these rises persisted for 300–500 years.

## Introduction

Measuring the age and elevation of late Quaternary reef-crest corals has enabled geoscientists to reconstruct the rate and magnitude of relative sea-level rise at several sites

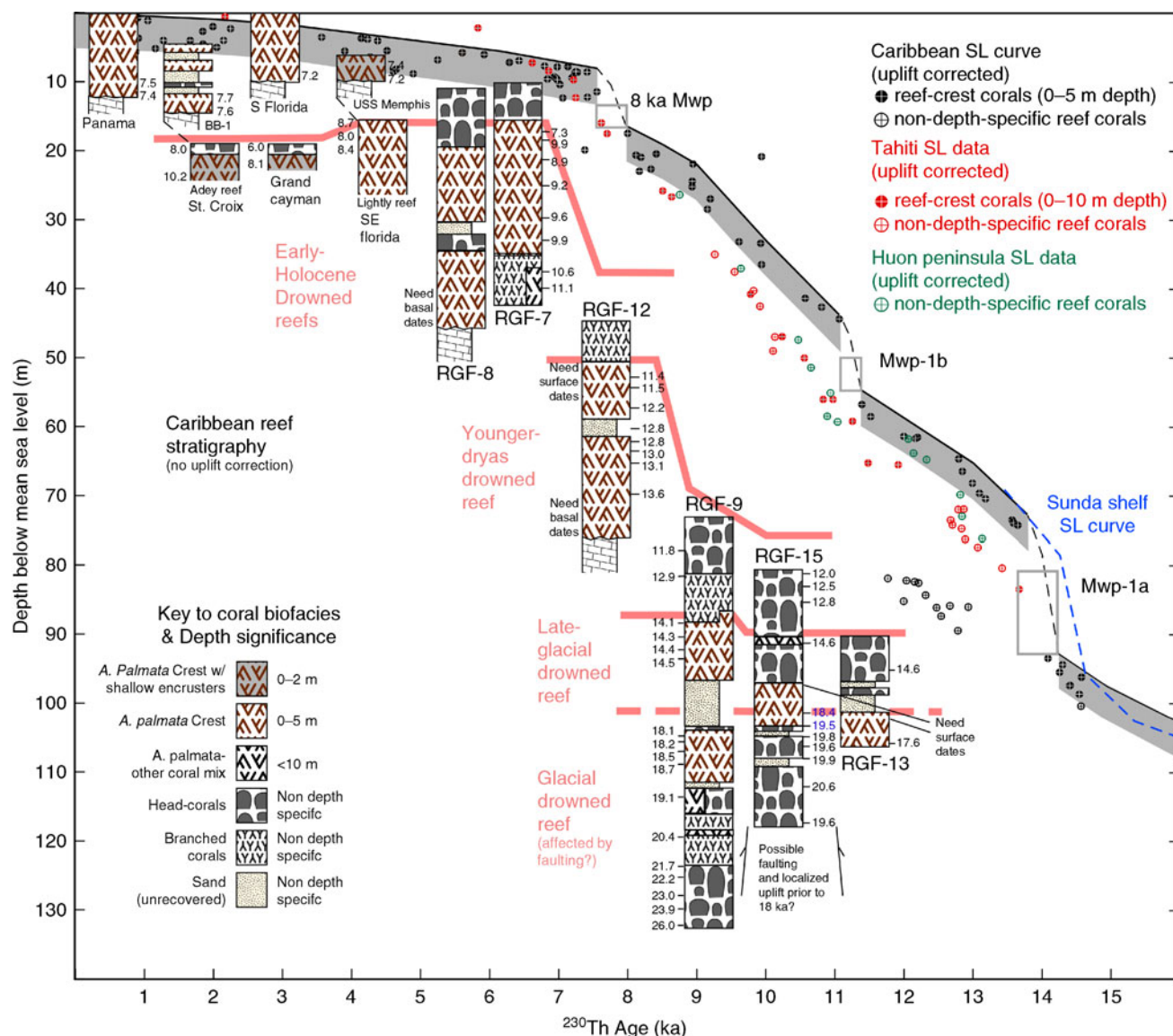
and identify global episodes of rapid sea-level rise that resulted from pulses of meltwater or iceburg discharge during the disintegration of ice sheets (Fairbanks, 1989; Blanchon and Shaw, 1995). These reconstructions show that the rate and magnitude of sea-level jumps were truly astonishing. Coastal and shallow marine ecosystems were inundated by rises of as much as 15 m at rates of up to 60 mm/yr. It is no surprise that understanding their causes and consequences has subsequently become the focus of a large multi-disciplinary research effort with particular emphasis on how they may relate to possible future rapid climate and sea-level change.

## Glacial Termination I (MIS-2)

Pulses in melt-water discharge during the last deglaciation were first reported by Fairbanks (1989) from an analysis of drowned reef-crest sequences cored off the south coast of Barbados. By plotting age/depth data from the reef-crest coral *Acropora palmata* in these cores and correcting them for tectonic uplift (0.34 mm/yr), he reconstructed sea-level rise during the last deglaciation between 17,100 and 7,800 radiocarbon years ago. From this curve, he identified two “exceedingly rapid” rise events separated by a period of reduced melting, and estimated that the first event, melt-water pulse 1a (Mwp-1a), was a rise of 24 m in less than 1,000 years centered at 12,000 radiocarbon years BP, and the second event, melt-water pulse 1b (Mwp-1b), was a rise of 28 m centered at 9,500 radiocarbon years BP. Fairbanks suggested that these rapid-rise events corresponded to the most intense phases of seasonal melt-water discharge during the disintegration of Northern Hemisphere ice-sheets, and estimated discharge rates of 14,000 km<sup>3</sup>/yr and 9500 km<sup>3</sup>/yr, respectively. In later studies, he and co-workers re-dated all samples using more precise <sup>230</sup>Th ages (Bard et al., 1990; Fairbanks et al., 2005) and produced a curve showing that Mwp-1a was centered at 14,000 years, with a period of reduced melting between 13kyrs and 11 kyrs, and Mwp-1b was centered at 11,000 years BP (Figure 1).

However, these meltwater pulses coincided with gaps between cores which led some to argue that they were artifacts resulting from non-uniform uplift, or from the post-growth collapse of reef deposits themselves (see discussion in Broecker, 1990; Bard et al., 1996; Radtke and Schellmann, 2006). To rule out this possibility, evidence of reef-drowning from other areas was required. That evidence was reported by Blanchon and Shaw (1995) who determined that elevations of drowned *A. palmata* reefs in the Caribbean-Atlantic reef province were consistent with the stepped pattern of sea-level rise identified from Barbados. By combining the previously reported coral ages with stratigraphic data, including the positions of *A. palmata* framework, intervening gaps, and the transitional thickness between units, they further constrained the timing, rate, and magnitude of these melt-water pulses and calculated that Mwp-1a was a 13.5 m rise in 290 years centered at 14,200 years, there





**Meltwater Pulses, Figure 1.** Three-step model of post-glacial sea-level rise in the Caribbean. Reconstruction of sea-level older than 8 ka uses uplift-corrected elevation and thickness of back-stepping *A. palmata* reef-crest sequences from Barbados (modified from Fairbanks, 1989; Blanchon and Shaw, 1995) and precise  $^{230}\text{Th}$  ages from corals in those sequences (Peltier and Fairbanks, 2006). Reconstruction of sea level younger than 8 ka is from stratigraphic sequences and calibrated radiocarbon-ages of relict and active Holocene reefs in tectonically stable areas of the Caribbean (Blanchon et al., 2002; Toscano and Macintyre, 2003). The position of mean sea level is constrained by maintaining coral age/elevation data within a 5 m envelope (shaded) which represents the 0–5 m reef-crest habitat depth zone where *A. palmata* forms a monospecific assemblage mixed with its clasts. Outliers are the result of either up-slope transport during storms or, in other areas, result from deeper habitat ranges for reef-crest corals. Correction for continuous uplift of Barbados is assumed to be 0.34 mm/yr but is ignored for quantification of the rate and magnitude of sea-level jumps that caused episodes of reef-crest drowning and back-stepping. Gray boxes show (non-uplift-corrected) age/elevation data gaps between reef-crest framework that are used to calculate minimum rate and magnitude of sea-level jumps; maximum magnitudes are calculated by assuming that sea-level position was 5 m higher than the base of up-slope reef-crest framework (as required by its 5 m depth habitat) and an increment of 5 m is added to the elevation gaps. Caribbean three-step model is contrasted with data from Tahiti, the Huon Peninsula, and the Sunda Shelf.

was a period of reduced melting between 13kyrs and 11 kyrs, and Mwp-1b was a 7.5 m rise in 160 years centered at 11,000 years (Figure 1). They also identified an additional melt-water pulse event at 7,100 radiocarbon

years that drowned early Holocene reefs below the 15 m isobath and led to the initiation of modern reefs above the 10 m isobath. Later calibration of these age data showed that this additional reef-drowning melt-water

pulse was centered at 8,000 calendar years (Toscano and Macintyre, 2003) and produced a rise of 6.5 m in <140 years (Blanchon and Shaw, 1995).

Subsequent attempts to test the 3-step model of Caribbean sea-level rise, and corroborate the existence, timing, and magnitude of melt-water pulses, have only been partially successful. The most successful sea-level reconstruction is from the Sunda Shelf between the Indonesian archipelago and the Vietnam peninsula (Hanebuth et al., 2000). Two core transects between the 126 m and 48 m isobaths recovered a transgressive sequence of organic-rich tidal-flat and mangrove-swamp deposits (Hanebuth and Statteger, 2003). Radiocarbon dating of in-situ organics above the Pleistocene basement allowed the reconstruction of sea level ( $\pm 1$  m) from 21 to 11 kyrs ago. This high-resolution reconstruction showed that Mwp-1a was recorded as a 16 m rise in 300 years starting at 14.6 calendar kyrs ago, almost identical to the rate and magnitude calculated from the Caribbean drowned reefs ( $13.5 \pm 2.5$  m in 290 years; Blanchon and Shaw, 1995). The only difference was the timing: on the Sunda Shelf Mwp-1a occurred 400 years before it did on Barbados (Figure 1). Although there has been considerable argument about which of these is correct (e.g., Weaver et al., 2003; Stanford et al., 2006), the difference in age between these sites may simply be the result of down-slope transport of younger *A. palmata* clasts onto the oldest drowned reef on Barbados seen at the top of core RGF-9 (Figure 1). Such a possibility could easily be tested by dating the lowest section of the up-slope reef (seen at the base of core RGF-12). Down-slope transport would cause an age overlap between the drowned and up-slope reefs.

Less precise reconstructions using corals with larger depth ranges have had more limited success. For example, a single core from the Huon Peninsula of Papua New Guinea recovered an uplifted 52 m thick coral sequence which recorded continuous reef accretion between 11,000 and 7,000 radiocarbon years BP (Chappell and Polach, 1991). All coral samples were later re-dated to obtain more accurate  $^{230}\text{Th}$  ages (Edwards et al., 1993) and corrected for tectonic uplift (1.9 mm/yr). The sea-level curve based on these new data showed a distinct period of reduced melting between 12.3 kyrs and 11.0 kyrs, followed by a clear Mwp-1b centered at 11 kyrs (Figure 1). It was claimed that the period of reduced melting prior to the meltwater pulse was shorter than at Barbados, but corals used to identify sea-level position at Huon have larger depth ranges than *A. palmata* and therefore are not as reliable in pinpointing the precise elevation of sea level (Chappell and Polach 1991). Also, the assumption that uplift was uniform in this highly-active neotectonic terrain cannot be confirmed.

Cores recovered from the modern reef-crest around the more tectonically-stable island of Tahiti found a thicker 90 m sequence of continuous reef accretion back to  $\sim 13,800$   $^{230}\text{Th}$  yrs BP (Bard et al., 1996; Montaggioni et al., 1997). This sequence therefore started accreting

immediately following Mwp-1a implying that its effects in Tahiti were the same as in Barbados, and that a rapid sea-level rise had caused reef drowning and up-slope reef back-stepping (Blanchon, this volume). As in the other records, the coral age/depth data, when corrected for subsidence (0.25 mm/yr) showed possible evidence for a period of reduced melting prior to Mwp-1b, but it was significantly shorter (11.5–11 kyrs) than that in either Barbados or PNG. Interestingly, however, the Tahitian corals consistently plot deeper than those at Barbados, indicating that they may not be as precise at indicating sea level as claimed (Blanchon, 1998). This is supported by two observations: the increase in offset of the Tahiti corals through time, and the pattern of shallowing of the cored reef sequence (Figure 1). Both observations indicate that the reef prograded after Mwp-1a so that, in a vertical core, progressively deeper reef-front corals were encountered through time. In other words, Tahitian cores represent deeper-reef accretion when compared to those in Barbados. New cores collected during the IODP-310 Tahiti Leg, should help determine if this offset is indeed the result of deeper coral growth or a function of differing glacio-isostatic-adjustment histories. One preliminary result so far indicates that Mwp-1a at Tahiti has a similar timing to that identified from the Sunda Shelf at 14.6 ka (Deschamps et al., 2009).

In addition to the deglacial events, evidence for a meltwater pulse at 8 kyrs (Mwp-1c) has also been further supported by additional discoveries of drowned reefs from Grand Cayman, southeast Florida and the Gulf of Carpentaria (Blanchon et al., 2002; Banks et al., 2007; Harris et al., 2008). On the east coast of Grand Cayman, a transect of short cores along the reef-front in 20 m of water recovered a submerged *A. palmata* reef-crest whose surface corals returned  $^{230}\text{Th}$  ages of between 8.9 kyrs and 8.1 kyrs BP (Blanchon et al., 2002). The depth of this drowned reef also corresponded with an intertidal notch on the western shelf at a depth of 18 m and indicated the establishment of an 18-m shoreline between 8.1 cal and 7.6 cal ka. Comparison of the age/depth data between Grand Cayman and other Caribbean islands, indicated a near synchronous demise and back-stepping of *A. palmata* reefs across the Caribbean around 8 kyrs ago in response to a rapid 6-m jump in sea level (Blanchon et al., 2002). But two potential problems with this jump hypothesis have been raised. The first problem was that back-stepping could only be demonstrated by comparing the age of reef drowning in one location with the age of up-slope reef initiation in another. In other words, there were few sites where clear evidence of both drowning and back-stepping had been reported together. That changed recently with the reporting of new age/depth data from an up-slope reef off the southeast Florida shelf (Banks et al., 2007). Combining the calibrated radiocarbon-age data of this new reef with those from an earlier report of an 8 ka old drowned reef further down-slope (Lighty et al., 1978), confirmed that at this site Mwp-1c at 8 kyrs caused the back-stepping of *A. palmata* reef crests 6–7 m up-slope in less than 580 years (Blanchon, this volume).

The second potential problem with the 8 ka jump was the discovery of a deposit of *A. palmata* off Sand Key, Florida, that apparently filled the elevation gap between drowned and back-stepped reefs (Toscano and Lundberg 1998; Figure 1). This deposit developed between 12.5 m and 9 m below present sea level and contained 9–7 ka old corals. In other words, it developed at the same time as the 8 ka old drowned reef reported 4–7 m further down-slope by Lighty et al., (1978). Given that Banks et al., (2007) confirmed that the down-slope reef morphology is directly analogous to that of modern Florida breakwater reefs, this means that Sand Key deposit further up-slope cannot also be a breakwater reef. This objection is supported by the fact that the deposit not only contains age reversals, but an 86 ka old extraformational clast reworked from the underlying foundation. The mismatch in elevation with coeval down-slope reefs, together with the evidence of reworking, clearly indicates that the Sand Key deposit is not of reefal origin but is a coastal boulder-rampart deposited by storms and hurricanes. As noted by Blanchon and Perry (2004), such problems highlight the importance of identifying in-place *A. palmata* reef framework using textural and taphonomic criteria in order to differentiate it from either boulder ramparts deposited up to 5 m above present sea-level, or submerged accumulations which can be deposited in much deeper water.

Until recently, there was scant support for reef drowning related to the 8 kyr Mwp-1c outside the Caribbean (e.g., Bard et al., 1996). But in 2008, Harris et al., reported early Holocene reef development in the Gulf of Carpentaria, northern Australia. Multi-beam sonar and short drill cores demonstrated widespread reef development between 23 m and 33 m water depth starting at 10.5 kys and ceasing by 8 kyrs. Unfortunately, the coral sequences were poorly developed and it is unknown if these reefs grew at sea level or were submerged below it. Their surface elevations however are remarkably consistent over wide areas indicating they were likely breakwater reefs. Evidence for the 8 ka Mwp-1c has also been reported from other sedimentary systems, notably deltas and estuaries (Stanley and Warne 1994; Bratton et al., 2003; Hori and Saito 2007) and isolation basins in glacio-isostatic rebound terranes (Yu et al., 2007).

### Last glaciation (MIS-3)

Reports of meltwater pulses prior to the last deglaciation are more controversial. For example, there have been multiple claims of melt-water pulses during the last Glacial between 19 ka and 65 ka. The first of these is a proposed melt-water pulse at 19 ka which is based on a core transect across the Bonaparte Gulf, in northern Australia between depths of 147 m and 34 m (Yokoyama et al., 2000). These cores recovered shelf and marginal-marine to brackish-water facies based on the foraminiferal and bivalve assemblages, which were used to radiocarbon date the sequence. Using age/depth data of the transition from the low-stand

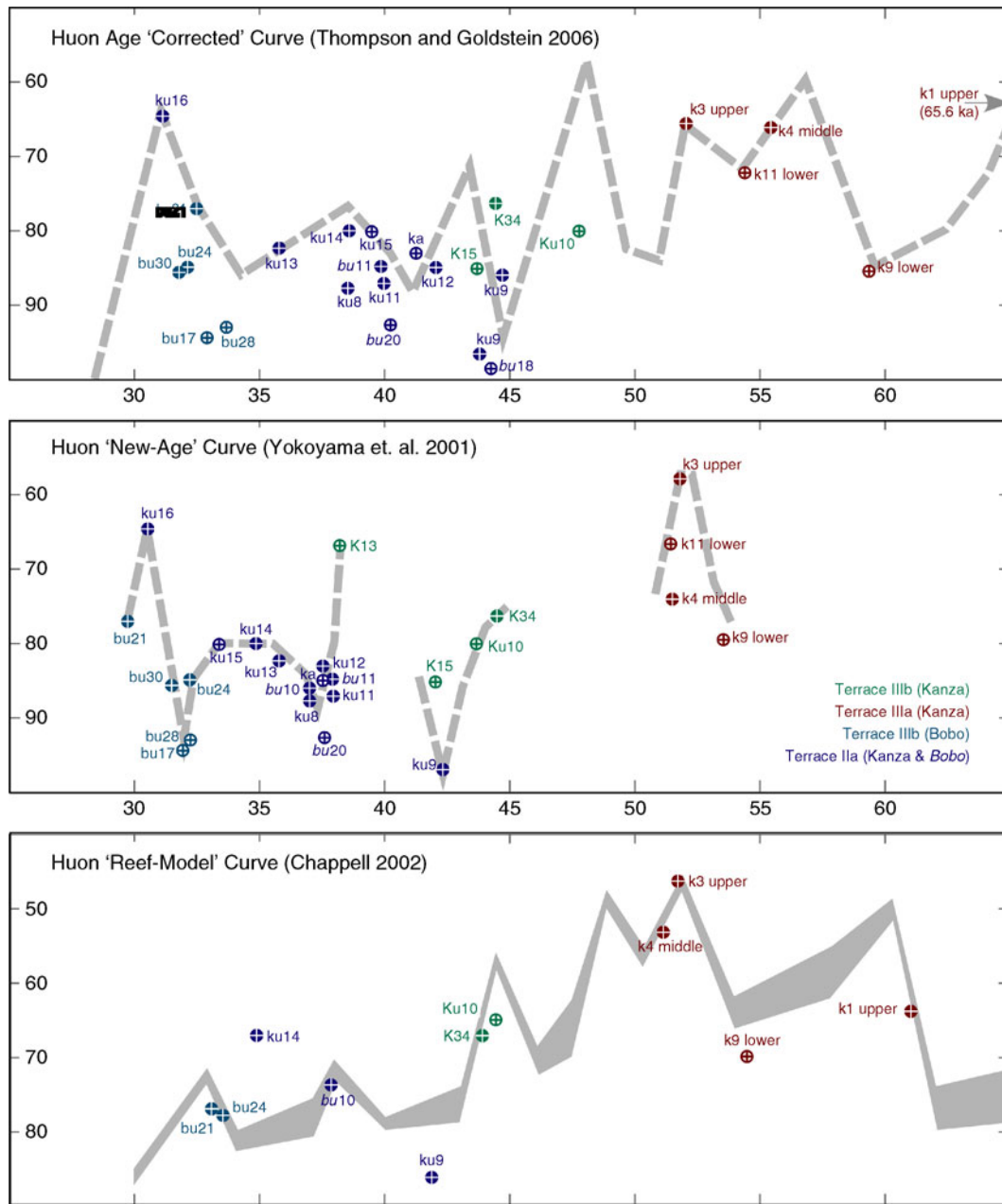
brackish-water facies into the succeeding marginal-marine facies, it was argued that meter-scale elevation differences between cores was the result of a melt-water pulse centered at 19 cal ka BP. The validity of this sea-level reconstruction, however, has been contested by Shennan and Milne (2003), who highlighted the presence of hiatuses reported in a later study (Yokoyama et al., 2001), inconsistencies between cores, and doubts concerning the depth range of the facies units. As a consequence, the interpretation of a meltwater pulse at 19 kyr is suspect.

The second report of a 19 ka meltwater pulse is from the north-east Irish coast where a presumed fluvial incision was filled by transgressive marine foraminiferal mudstones along a coastal area undergoing active glacio-isostatic uplift (Clark et al., 2004). The uniform age of these deposits and the apparent transgression over a fluvially-incised subaerial surface were interpreted to result from a rapid 10 m rise in sea level at 19 cal ka BP. Unfortunately, alternative interpretations of the origin of the incised valley, such as marine ravinement, cannot be ruled out. In addition, the correction of the ages for marine reservoir has been disputed by Hanebuth et al., (2009). Such problems once again render the interpretation of a meltwater pulse at 19 ka as ambiguous.

Further reports of fully Glacial (MIS-3) stage meltwater pulses have come from the Huon Peninsula. There, the ages of uplifted reef terraces between 30 ka and 65 ka apparently matched rapid climate changes and ice-sheet events seen in Greenland ice and north Atlantic sediment cores (Chappell, 2002). A sea-level reconstruction from these terraces used the thickness and geomorphology of reef-crest and intertidal units to model the relative rate and magnitude of sea-level rise by making assumptions about reef type and accretion rate. Then, these relative rises were used to reconstruct absolute sea-level position using  $^{230}\text{Th}$  ages of the reefs and applying uplift corrections (Figure 2). This preliminary reconstruction showed 5 rapid sea-level-rise events of between 10 m and 20 m within duration of 1–2 ka; the timing of some of these rises coincided with rapid-ice loss events from the Laurentide Ice Sheet, known as Heinrich events (Hemming 2004).

Further dating of the Glacial reef terraces on the Huon Peninsula by Yokoyama et al., (2001) attempted to provide an independent sea-level reconstruction and model glacio-isostatic adjustment (Figure 2). Unfortunately, this new reconstruction conflicted in terms of timing, number, and magnitude of rapid sea-level rise events with the reconstruction of Chappell (2002). This is largely because Yokoyama et al., (2001) ignored the problem of true-age variability (Scholtz and Manginni, 2007) and considered all isotopically-reliable ages to be valid sea-level indicators, despite their lack of stratigraphic consistency. These errors were compounded by making an age-dependant uplift correction for every dated coral, rather than making this correction for a core-group of ages that best represented the time-span of individual reef-crest development. Together these errors led to single outlying ages forming the peaks of rapid sea-level-rise events, and





**Meltwater Pulses, Figure 2.** Three sea-level reconstructions for the Huon Peninsula's Glacial coral-reef terraces (Terraces II and III). Lower reconstruction is based on a model of reef thickness, type, and accretion rate estimates, corrected for uplift using average  $^{230}\text{Th}$  age of individual terraces (Chappell, 2002). Middle reconstruction based on new  $^{230}\text{Th}$  ages (Yokoyama et al., 2001) with each age corrected for uplift. Upper reconstruction is based on correction of all  $^{230}\text{Th}$  ages for open system effects (Thompson and Goldstein, 2005) with each age corrected for uplift. Correcting each age for uplift introduces serious errors and results in single outlying anomalous ages forming the peaks of rapid sea-level-rise events, and neighboring ages from the same reef being placed in different parts of the sea-level curve. In other words, curve position is an artifact of dating which results from true-age variability of samples.

neighbouring ages from the same reef being placed in different parts of the sea-level curve (e.g., ku16 and k13 in Figure 2). In other words, this implies that a single conformable reef unit developed during different stages as

sea level returned to the same position over time. Later, Esat and Yokoyama (2006) claimed that this 'disorderly growth conjecture' was a valid explanation of reef development, rather than addressing the more plausible

explanation that  $^{230}\text{Th}$  ages are difficult to replicate on sub-millennial timescales, as shown by the fact that 50% of ages with pristine isotopic values can have discordant  $^{231}\text{Pa}$  ages (Scholz and Mangini, 2007). In addition, disorderly growth is clearly untenable in conformable reef sequences, given that multiple passes of the shore-face would leave significant stratigraphic evidence of marine erosion and/or subaerial exposure.

The problem of true-age variability in the ages of Yokoyama et al., (2001) was partially addressed by Thompson and Goldstein (2005) who recalculated them to correct for bias introduced by open-system diagenesis. Although this reduced the spread of ages from some reef units, it did not significantly alter outlying ages, which remained stratigraphically inconsistent and again plotted in separate parts of the sea-level curve (Figure 2). This failure to address fundamental stratigraphic consistency of these age data and to continue making erroneous age-dependant uplift corrections on every dated coral seriously compromises the Glacial sea-level reconstruction of Thompson and Goldstein (2005) and means that the sea-level peaks are merely dating artifacts.

### Glacial Termination II (MIS-6)

Reports of meltwater pulses during the penultimate deglaciation (MIS-6) have also recently been made. On the Huon Peninsula, Esat et al., (1999) reported that a cave exposing the base of the last interglacial terrace (VII) some 90 m below its crest, contained in-situ corals with 1-cm-thick annual bands, implying growth in a shallow-water reef. These corals returned seven isotopically acceptable  $^{230}\text{Th}$  ages of between 125.6 ka and 133.7 ka (i.e., a 7.2 ka true-age variation) which were averaged to give an age of  $130 \pm 2$  ka (a process which excluded a reliable age of 115 ka). This was compared with a  $134 \pm 2$  ka age average from four corals recovered from 5 to 12 m below the reef-crest reported earlier by Stein et al., (1993), but four significantly younger ages at 2 and 16 m were ignored. By comparing average ages and elevations of these two coral groups, Esat et al., (1999) claimed that sea-level fell rapidly at least 70 m from the level of the 134 ka crest group, and then rose rapidly at least 85 m from that of the 130 ka cave group, with both the fall and the rise occurring within the 4 ka difference between the age groups. Unfortunately, the comparison between these two groups is questionable given that it ignores younger ages from both the down-slope cave site and the up-slope barrier site reported earlier by Stein et al., (1993). It is much more likely that the stratigraphic age inversions at both sites reflect true-age variability (Scholz and Mangini, 2007) and that neither may be accurate (Blanchon, this volume). In the absence of reliable ages, the stratigraphy dictates that the cave is simply the oldest part of terrace VII which accreted vertically as sea-level rose. As a result, claims of a rapid 70 m fall and an equally rapid 85 m rise at the Huon Peninsula during the penultimate deglaciation are extreme and poorly supported by the data.

Similar claims of extreme sea-level variability have also been made from IODP-310 cores recovered from the fore-reef slopes of Tahiti (Thomas et al., 2009). In these cores, two corals recovered from 115 to 118 m below present sea level returned reliable  $^{230}\text{Th}$  ages of 133 and 137 ka respectively. Both corals are typical of shallow-water reef environments but are separated by a 30 cm section of much deeper-reef framework. This led Thomas et al., (2009) to claim that a rapid deepening event drowned the older coral and produced a limited deep reef before sea-level fell rapidly leading to a resumption of shallow reef development. In other words, the return to shallow reefal environments represented a reversal in the rapidly rising sea level during the penultimate deglaciation. Unfortunately, such an interpretation ignores the more plausible possibility that the shallow-water corals were in fact clasts transported down-slope into deeper water. Examination of the cores in their Figures S2 and 3 supports this shallow-clast interpretation, with the deeper coral at 118 m consisting of a 5 cm diameter coral clast enclosed by other basalt- and coral-clasts (which were even identified as clasts in the log description). The other coral, which sits directly on top of the deeper framework, could also be a clast given its small size (20 cm); the fact that it contains surfaces encrusted by coralline algae, upward growth, and apparently horizontal cavity fills could merely be coincidental, indicating it fortuitously landed with an upright orientation. However, a clast interpretation is supported by the lack of coral microbialites which are typical of deglacial reef-framework of Tahiti (Heindel, 2008). Regardless of the interpretation chosen, such extraordinary claims of extreme sea-level changes are clearly not supported by adequate data. As such, the existence of meltwater pulses during the penultimate deglaciation, although likely, remains to be proven by credible reef data.

### Last Interglacial (MIS-5e)

A better supported claim of a more modest meltwater pulse has recently been made from reef development on the Yucatan Peninsula during the last Interglacial (MIS-5e). There, Blanchon et al., (2009) identified an episode of reef-crest demise at +3 m and back-stepping to +6 m. In some parts of the reef, this back-stepping was accompanied by erosion, but in others the sequence between the two reefs was continuous, implying that they grew consecutively on an ecological timescale with no intervening hiatus (Figure 4). In turn, this consecutive development requires that reef-crest back-stepping occurred on an ecological timescale, implying that it was caused by a 2–3 m sea-level jump (Blanchon, 2010). Although the dating precision precluded testing the rise rate, a test of the stratigraphic relations was made by dating samples from both reef-crests. Unfortunately, only the +6 m crest returned strictly reliable  $^{230}\text{Th}$  ages which fell between 119.5 ka and 117 ka. However, these ages were younger than well-dated +3 m reefs that had developed in other areas,

**Meltwater Pulses, Table 1** Summary of evidence for meltwater pulses, their timing, rate, and magnitude

| Mw-event            | Site (ref.)              | Depth (m)   | Adj. depth (m)     | Magnitude (m) | Adj. magnitude (m) | Timing (kyrs)    | Duration (years) | SL rise rate (mm/yr) |
|---------------------|--------------------------|-------------|--------------------|---------------|--------------------|------------------|------------------|----------------------|
| Mwp-1a              | Barbados <sup>b</sup>    | 87 to 76–71 | <b>93 to 78–73</b> | <b>11–16</b>  | 11–20              | 14.1–13.7        | 450              | 24–36                |
| Mwp-1a <sup>a</sup> | Barbados <sup>b</sup>    | 90 to 76–71 | <b>95 to 80–75</b> | <b>14–19</b>  | 15–20              | <b>14.6–14.3</b> | 300              | <b>47–63</b>         |
| Mwp-1a              | Sunda Shelf <sup>c</sup> | 96–93 to 80 |                    | 13–16         |                    | 14.6–14.3        | 280              | 46–57                |
| Mwp-1b              | Huon Pen. <sup>d</sup>   | 32–25       | <b>53–46</b>       | 7             | <b>7</b>           | <b>11.1–10.7</b> | 372              | 19                   |
| Mwp-1b              | Barbados <sup>a</sup>    | 51 to 46–41 | <b>55 to 50–45</b> | 5–10          | <b>5–10</b>        | <b>11.4–11.1</b> | 314              | 16–32                |
| Mwp-1b              | Tahiti <sup>c</sup>      | 66–59       | <b>65–59</b>       | 7             | <b>6</b>           | <b>11.5–11.3</b> | 215              | 28                   |
| Mwp-1c              | Caribbean <sup>b</sup>   | 18 to 13–9  |                    | 5–9           |                    | 8.0–7.6          | 400              | 13–23                |
| 121 ka Mwp          | NE Yucatan <sup>f</sup>  | +3 to +5–6  |                    | 2–3           |                    | 121              | <100             | 20–30                |

<sup>a</sup>excluding upper *A. palmata* unit in RGF-9 due to suspected downslope transport from RGF-12

References for column two: <sup>b</sup>Blanchon (Reef Backstepping, this volume) updated from Blanchon and Shaw (1995), using new data from Toscano and Macintyre (2003) and Peltier and Fairbanks (2006); <sup>c</sup>from Hanebuth et al. (2000) and Hanebuth and Stattegger (2003);

<sup>d</sup>Edwards et al. (2003); <sup>e</sup>recalculated from Bard et al. (1996); <sup>f</sup>Blanchon et al. (2009).

both supporting the stratigraphy and constraining the sea-level rise to around 121 ka. To confirm these results however requires replicating the back-stepping reef stratigraphy and obtaining a reliable chronology in other stable areas.

### Origin of meltwater pulses

The preceding review of individual claims of meltwater pulses shows that solid geological evidence exists only for the 3 jumps in sea level during the last deglaciation at 14.6, 11.4 and 8 ka. Preliminary evidence also exists for a jump at the end of the last Interglaciation around 121 ka, although this requires support from other stable areas. Tabulation of these data shows that the average rise-rate during these jumps was as much as 63 mm/yr (Table 1). In other words, the jumps represent a rise-rate that is as much as 6 times the background deglacial rise-rate and therefore clearly implicate major rapid ice-loss events resulting from ice-sheet collapse (Blanchon and Shaw, 1995).

Linking the timing of sea-level jumps with climatic evidence of ice-sheet instability, however, is hindered by age biases in both marine-radiocarbon and ice-core chronologies (Skinner, 2008; Druffel et al., 2008). Despite such biases, recent improvements in synchronizing ice-core chronologies indicate that meltwater pulses coincide with or closely follow abrupt climatic warming, which was itself preceded by severe cooling episodes, known as Heinrich events, caused when the Laurentide Ice Sheet extended out to the edge of the continental shelf (see Hemming, 2004). For example, the start of Mwp-1a on the Sunda Shelf and Tahiti at 14.6 ka coincides with or closely follows the abrupt onset of Bolling/Allerod warming in the NorthGRIP ice core at 14.7 ka (Steffensen et al., 2008), which is itself preceded by Heinrich event 1 from 14.5 to 17.5 ka (Skinner, 2008). Similarly, Mwp-1b on Barbados, which starts at 11.4 ka, closely follows the abrupt onset of PreBoreal warming in NorthGRIP at 11.7 ka. However, further dating of the base of the

reef-crest sequence in RGF-8 might push the onset of Mwp-1b closer to the ice-core timing (Figure 1). Finally, the timing of Caribbean reef demise at ~8 ka closely follows the onset of warming after the 8.2 ka cold event seen in Greenland ice-cores, and the rapid disintegration of the Laurentide Ice-sheet between 8.2 ka and 8.5 ka (Barber et al., 1999; Carlson et al., 2008). If this phasing between rapid sea-level rise events and abrupt climate warming is confirmed, it will have serious implications for the future stability of remaining ice-sheets under the ongoing episode of anthropogenic global warming.

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## Cross-references

[Back-Stepping](#)  
[Last Interglacial and Reef Development](#)  
[Postglacial Transgression](#)

## MICRITE

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### Synonyms

[Microcrystalline calcite](#)

### Definition

Micrite is a textural term for microcrystalline carbonates less than 4  $\mu\text{m}$  in size.

### Introduction

The term “micrite” is a contraction of the words “microcrystalline calcite” and was introduced by Folk (1959, p. 8) as an aid in the classification of limestones. Initially, Folk applied the term to microcrystalline calcite ooze in the size range of 1–4  $\mu\text{m}$ . Adding a prefix, he coined terms such as “biomicrite” to refer to fossils in a microcrystalline matrix. In 1974, Folk expanded the meaning of the term “micrite” to encompass all carbonate minerals measuring 1–4  $\mu\text{m}$ . He also added a new term “minimicrite” for sizes less than 1  $\mu\text{m}$ .

Bathurst (1966) applied Folk’s terminology to refer to the process of grain surface alteration to micrite caused by microborings filled with micrite precipitates as “micritization”. However, Friedman (1985) thought that Bathurst and others who used his terminology (e.g., Lloyd, 1971; Gunatilska, 1976; Kobluk and Risk, 1977) were misusing Folk’s terminology that simply referred to a microcrystalline ooze matrix.

It was Alexandersson (1972) who suggested that “micrite” should be a textural term to cover all microcrystalline carbonates. Most subsequent studies of grain alteration or submarine lithification use both “micrite” and “minimicrite” as textural terms (e.g., Land and Moore, 1980; Macintyre and Marshall, 1988; Reid et al., 1992; Reid and Macintyre, 1998; Macintyre and Reid, 1995, 1998).

### Conclusion

In carbonate petrographic studies, the terms micrite (4–1  $\mu\text{m}$ ) and minimicrite (<1  $\mu\text{m}$ ) should be used as textural terms to refer to all microcrystalline carbonates.

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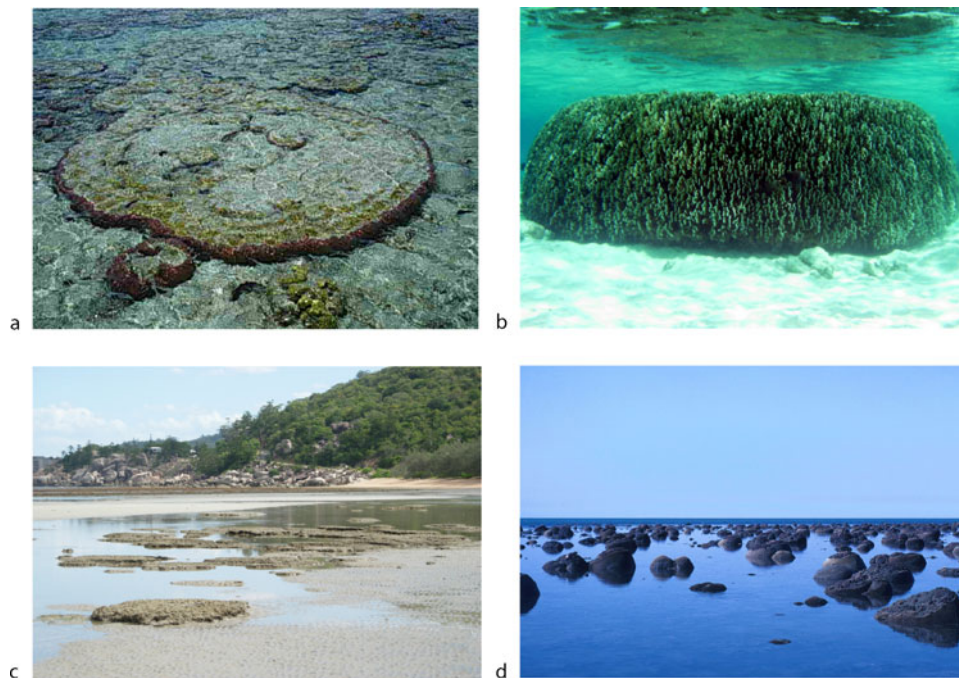
[Aragonite](#)  
[Calcite](#)  
[Platforms \(Cemented\)](#)  
[Porosity Variability In Limestone Sequences](#)  
[Submarine Lithification](#)

## MICROATOLL

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### Definition

Microatolls are intertidal coral colonies with dead, relatively flat, upper surfaces surrounded by an annular rim of living coral (Figure 1a,b). They form when upward coral growth is constrained by prolonged exposure near to shallow water, but polyps on the colony sides remain alive and continue to grow laterally (Scoffin and Stoddart, 1978; Stoddart and Scoffin, 1979; Woodroffe and McLean, 1990). Fossil microatolls are microatolls in which no living polyps survive but the colony morphology is preserved (Figure 1c).



**Microatoll, Figure 1** (a) Living *Porites lutea* microatoll with multiple ringed morphology, reef flat, Cocos Keeling Islands, eastern Indian Ocean; (b) *Heliopora coerulea* microatoll, reef flat Mendhoo, Maldives; (c) Fossil microatolls 4000–5000 years old, Magnetic Island, GBR, Australia; (d) Heliotropic *Goniastrea retiformis* microatolls, Paluma Shoals, GBR, Australia.

## Introduction

Darwin (1842) first described coral microatolls, with further accounts by various other early reef scientists (e.g., Dana, 1872; Semper, 1880). Guppy's (1889) description of “miniature atolls” from the Cocos (Keeling) Islands first compared the living coral annulus on microatolls to the circular reef rim of coral atolls, followed by Agassiz (1895) and Krempf (1927) who referred to microatolls as “diminutive atolls” and “dwarf atolls” respectively. The specific term microatoll was coined by Wood-Jones (1910) who argued that microatolls resemble coral atolls and form because sedimentation restricts coral growth to their peripheral rim, as he proposed in his largely discounted theory of atoll formation. Abe (1937) referred to microatolls as “table-forming corals”, emphasizing their flat dead tops.

Patch reefs composed of multiple coral colonies with raised rims and sand-filled centres have been referred to as microatolls (e.g., Kornicker and Boyd, 1962; Larkum and Steven, 1994), but are better described as “mini-atolls” (Scheer, 1971). Thirty years ago, Scoffin and Stoddart reviewed “the nature and significance of microatolls” and recommended that only single coral colonies be described as microatolls (Scoffin and Stoddart, 1978; Stoddart and Scoffin, 1979). This has been applied with only rare exceptions. The focus of these earlier investigations was almost entirely on microatolls as high quality sea-level indicators

(see Chapter *Sea-Level Indicators*), an application improved further by recent technological advances that have increased the resolution of elevation survey and radiometric dating. Further, exceptional palaeoenvironmental records preserved in the geochemistry and structure of microatoll skeletons are being discovered, and represent exciting new areas for research.

## Microatoll description

Most microatolls develop from massive corals; however, branching and foliaceous corals may also adopt this morphology. *Porites* microatolls are particularly common, and intertidal *Goniastrea* and *Platygyra* colonies also form microatolls on many reefs (Figure 1d). They are most abundant on Indo-Pacific reefs but also occur in the Caribbean. In the most detailed survey to date, 43 species from 23 genera were identified as forming microatolls in the northern Great Barrier Reef (GBR) (Rosen, 1978). Microatolls are usually less than 0.5 m high (vertical thickness) but they can be long-lived growing to several meters in diameter. Massive *Porites* grow at rates of around 1 cm per year, so microatolls of a meter in diameter are typically around 40–50 years old. A fossil microatoll exceeding 9 m in diameter and dated at  $2195 \pm 80$  years BP at its centre and  $1535 \pm 130$  years BP on its margin occurs on Pagan in the Mariana Islands (Siegrist and Randall, 1989), with a similarly large fossil *Porites*



(9.6 m diameter,  $7009 \pm 41$  cal years BP at centre) reported from the Leizhou Peninsula, in the southernmost part of Guangdong province in southern China (Yu et al., 2009). *Porites compressa* microatolls 7 m in diameter occur in Kaneohe Bay, Hawaii (Roy, 1970), and fossil *Porites* microatolls 6 m in diameter occur at several locations on the GBR (Hopley and Barnes, 1985; Hendy et al., 2003). Large microatolls demonstrate continuity of growth for several centuries, but most microatolls are  $< 2$  m in diameter. This probably reflects the relatively low probability of extended survival in shallow reef environments where corals are most vulnerable to a range of debilitating conditions. Microatolls on the northern GBR surveyed by Scoffin and Stoddart (1978, p.105) averaged 0.5 m in diameter, although other than stating that they “vary in size from a few centimeters to a few meters” no statistical description of the variance was offered.

### Microatoll formation

Corals develop into microatolls when prolonged emergence during low tides kills polyps on a colony’s upper surface and constrains subsequent growth to its sides. Tolerances to emergence vary with species; *Goniastrea* and *Platygyra* typically grow higher than *Porites* when they occur on the same reef flat. Other factors have been argued as drivers of upper surface mortality and microatoll formation, including excessive sedimentation (Wood-Jones, 1910), nutrient dynamics, and hydrodynamic stress (Stoddart and Scoffin, 1979); however, the general symmetry developed by individual microatolls and the accordant morphologies developed by neighboring microatolls are difficult to reconcile with these typically and unevenly distributed stresses. Subaerial emergence is clearly the main environmental parameter driving the formation of microatolls in most shallow reef settings, where the absolute elevation of the upper limit to coral growth is a function of the duration of exposure and the intensity of desiccating conditions, which are strongly influenced by elevation relative to a tidally modulated water level. Where microatolls grow in “open water” habitats freely connected to the open ocean, the confining water level is a tidal datum that can be linked to sea level. However, where the ebbing tide is impeded as it drains off the reef, the confining water level is moated above the open water level (see Chapter *Moating*) and thus the upper limit to coral growth is controlled by the height of the moat sill, and is less precisely tied to sea level (Hopley and Isdale, 1977).

The relationship between the upper limit to coral growth and tidal levels may vary with exposure to factors such as wavelet wetting, diurnal, and seasonal tidal patterns, but on the central GBR, where the mean tidal range is 2–3 m, the tops of microatolls within the same field are usually within  $\pm 10$  cm (Chappell et al., 1983). Smithers and Woodroffe (2000) indicate that even greater uniformity is found where the tidal range is smaller, such as at the microtidal Cocos (Keeling) Islands, although even

there microatoll elevations may vary by as much as 40 cm between different habitats (reef flat, intertidal passage, lagoonal) that experience different hydrodynamic conditions. The tops of *Porites* microatolls in open-water habitats on the GBR are usually close to the mean low water spring (MLWS) tide level, but may extend to the mean high water neap (MHWN) tide level in moated habitats (Scoffin and Stoddart, 1978). In the Cocos (Keeling) Islands the tops of open water microatolls are typically elevated approximately midway between MLWS and MLWN.

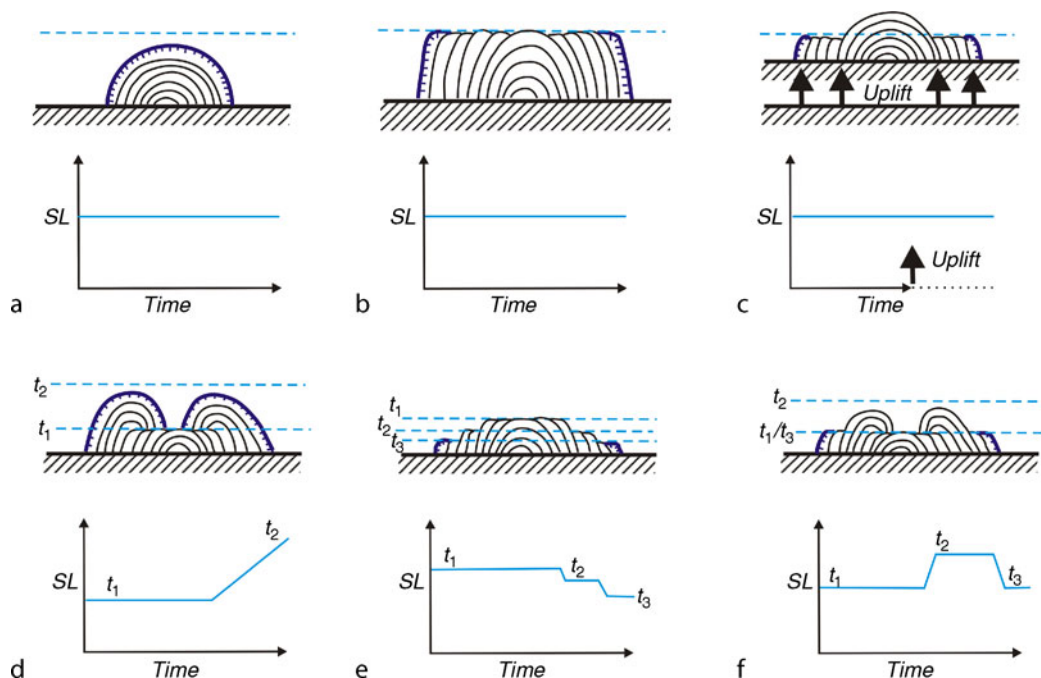
The relatively flat top developed by coral microatolls is referred to as the microatoll plane (Scoffin and Stoddart, 1978). This surface is rarely perfectly horizontal as the water level which confines upward coral growth is seldom absolutely constant through time. As water levels and the upper limit to coral growth fluctuate over a microatoll’s lifetime, complex microtopographies composed of concentric ridges and swales can progressively develop across the microatoll plane. Hopley (1982) identified four common microatoll forms:

1. “*Classical*” microatolls are the basic discoidal kind, with a relatively flat microatoll plane formed under relatively stable water level;
2. “*Top hat*” microatolls have an elevated centre and lower outer rims. They form where the upper limit to coral growth is abruptly lowered, for example, where a storm breaches the sill of a pond that holds water over the reef flat at low tide (Hopley and Isdale, 1977);
3. “*Uprgrown*” microatolls have low centres encircled by higher living rims. They form where the confining water level has risen, as might occur if falling tides are moated behind a rubble rampart deposited on a reef flat during a storm, or where the reef is subsiding (possibly driven by compaction, or tectonic subsidence);
4. “*Multiple-ringed*” microatolls with concentric undulations across the microatoll plane form when the upper limit to coral growth has oscillated through time, either episodically or dynamically, as may occur where interannual variations in sea level forced by relatively rapidly changing oceanographic and atmospheric conditions – such as ENSO – are experienced.

The progressive development of different microatoll surface morphologies driven by temporal changes in the water level that limits upward coral growth is shown schematically in Figure 2.

### Microatolls and sea level

Where the confining water level is an open water level, this relationship means that microatolls, or collections of microatolls, can be used to reconstruct sea-level histories that spatially and temporally augment those available from instrumental records (see Chapter *Sea-Level Indicators* for diagrams). Microatoll derived sea-level records are generally of two main types: (a) records of mid-late Holocene sea level constructed by comparing the elevations of radiometrically dated fossil microatolls to the



**Microatoll, Figure 2** Schematic cross-sections through microatolls showing progressive development (rings are annual growth rings with most recent growth at living margins), with water level history below. (a) Hemispherical coral as yet unconstrained by emergence at low tide and not yet adopting the microatoll form; (b) “Classical” microatoll developed under relatively stable water level; (c) hemispherical coral transformed into a microatoll after emergence caused by tectonic uplift; (d) “Upgrown” microatoll developed under rising water level conditions; (e) “Top hat” or terraced microatoll recording falls in constraining water level; and (f) “Multiple-ringed” microatoll formed by confining water level that fluctuates both upwards and downwards (after Hopley 1982; Woodroffe and McLean, 1990).

elevation of living microatolls at the same location with a known relationship to a tidal datum; and/or (b) records of interannual or decadal sea-level change reconstructed from detailed analyses of the surface topography of long-lived microatolls or microatolls with overlapping lifespans. Both assume that the tidal datum that is the confining water level is unchanged and as sea level varies the absolute elevation of this tidal datum fluctuates.

In many locations, fossil microatolls, often 5,000–6,000 years old, can be readily identified and compared directly with nearby living counterparts that can be surveyed to a tidal datum. Where the tidal curve has not significantly changed, the relative elevations of microatoll tops document the heights of former constraining water levels. Radiometric dating of the fossil microatolls at different heights assigns a chronology to these water levels (see Chapter *Uranium Series Dating*). Where it is confirmed that fossil microatolls were not moated, these histories of water-level change are also excellent records of sea-level change. This approach has been applied to establish mid-late Holocene sea-level histories on the Central GBR (Chappell et al., 1983), in Torres Strait (Woodroffe et al., 2000), the Pacific (e.g., Nunn, 2000; Goodwin and Harvey, 2008), and Indian Oceans (e.g., Woodroffe and McLean, 1990; Kench et al., 2009).

Microtopographic undulations over the upper surfaces of well-preserved microatolls track interannual variations in the elevation of the confining water level (Woodroffe and McLean, 1990; Smithers and Woodroffe, 2001). The internal skeletal structure of massive microatolls contain annual density bands (see Chapter *Sclerochronology*) that can be used to age the upper limit to coral growth over the microatoll’s lifetime (preserved as the topography of the microatoll plane), usually by counting back the density bands from the living edge at the time of sampling. Rapid rises that exceed maximum coral growth rates will not be fully recorded, but microatoll microtopographies may yield detailed sea-level records extending back decades and centuries in modern corals (Woodroffe and McLean, 1990; Smithers and Woodroffe, 2001; Spencer et al., 1997), and also in well-preserved fossil microatolls of mid-Holocene age (Yu et al., 2009).

### Microatoll records of ENSOs, earthquakes, and other environmental conditions

Microatolls are also excellent archives of a range of other environmental conditions. These include the following:

- (a) El-Nino Southern Oscillation (ENSO) events: Sea-level changes accompany shifts from El Nino to La

Nina conditions and associated ENSO cycles, and it has been demonstrated that microatolls in the Pacific Ocean preserve smoothed records of these oscillations across their upper surfaces (Woodroffe and McLean, 1990; Spencer et al., 1997; Woodroffe and Gagan, 2000). The records are smoothed because the record is biologically mediated and only rises in sea level below the coral growth rate ( $\sim 1\text{--}2$  cm a year for massive *Porites*) can be completely recorded. Furthermore, in mid-ocean settings changes in sea surface temperature (SST) and salinity (SSS) related to ENSO are documented by the geochemistry of microatoll skeletons (see Chapter *Palaeoclimate from Corals*), with high fidelity between adjacent corals (Woodroffe and Gagan, 2000). Concerns that geochemical records from microatolls may not represent oceanic water conditions appear allayed by studies that demonstrate excellent correlations between these geochemical records and instrumental SST datasets. Narrow stress bands may also be deposited in microatoll skeletons when conditions for coral growth become critical – and these may document the occurrence of past severe ENSO or other stress events.

- (b) Tectonic movements and event prediction: Microatolls respond to relative sea level and thus their surface morphologies reflect not only fluctuations in the sea surface but also movements of the substrates on which they grow (see Figure 2c). Microatolls in tectonically active areas have been used to establish histories of subduction or uplift associated with earthquakes or more subtle interseismic crustal deformation processes (Taylor et al., 1987; Zachariasen et al., 2000; Natawidjaja et al., 2004, 2006, 2007; Briggs et al., 2006), to investigate spatial patterns of plate rupture during single and multiple events (Konca et al., 2008), and to calculate the rates of tectonic stress accumulation, the frequency of past tectonic events, and the probability of future tectonic hazards (Sieh, 2006; Sieh et al., 2008). For example, Briggs et al. (2006) used GPS measurements of coral microatolls to establish abrupt coseismic uplift of reefs at Nias by as much as 3 m during the Great 2005 Nias-Simeulue earthquake, which followed decades of strain accumulation and submergence, documented by the development of “upgrown” microatolls.
- (c) Other environmental parameters: Coral microatolls confirm that a reef has reached sea level and are critical evidence in geomorphological investigations of reef structure and growth. For example, fossil microatolls across reef flats can reveal reef flat progradation histories (Smithers et al., 2006). Storm histories can also be derived from microatolls, either from upper surface patterns of moated microatolls where moat height or integrity (and thus moated water level) is affected by storms (Hopley and Isdale, 1977) or where storms cause tilting of the microatoll plane (relative to the pre-storm alignment), the timing of which can be derived from the colony’s internal structure. Some

microatolls grow in areas where tidal conditions only expose the coral during daylight at a particular time of year. For example, on the Central GBR daytime low spring tides only occur during the winter months, when the sun is in the northern sky. As a result, higher growing microatolls, such as those formed by *Goniastrea* and *Platygyra*, develop tilted tops in which the northern, more directly radiated section of the living rim is lower than the “lee” side (Figure 1d). Buskirk et al., (1981) reported similar microatolls with tops dipping towards the sun from Vanuatu. This pattern is usually developed across entire microatoll fields, and where storms have affected these reefs, disturbance of this pattern is conspicuous.

## Summary

Coral microatolls are excellent sea-level indicators. Advances in survey and radiometric dating technologies that have improved both elevational and temporal resolution have further enhanced their utility. Furthermore, in recent decades researchers have discovered that microatolls yield excellent data on a broader range of environmental phenomena including atmospheric, oceanic, and tectonic processes. These high-resolution datasets augment more recent and scattered instrumental records both spatially and temporally, improving knowledge of the natural variability and significance of recent changes in these parameters.

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## Cross-references

Atolls  
 Cocos (Keeling) Islands  
 Earthquakes and Emergence or Submergence of Coral Reefs  
 El Niño, La Niña, and ENSO  
 Great Barrier Reef Committee  
 Moating  
 Paleoclimate from Corals  
 Radiocarbon (<sup>14</sup>C): Dating and Corals  
 Sea-level Indicators  
 Sclerochronology  
 Uranium Series Dating

## MICROBES

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### Definition

Microbes are microscopic organisms. Many organisms fit into this size category, including, Bacteria, Archaea, Fungi, Protists, etc. The definition provided here uses microbes to describe Bacteria and Archaea. These two groups are unicellular organisms, which do not contain a nucleus and rarely harbor membrane-bound organelles. Both Bacteria and Archaea were classified together as Prokaryotes, but this classification is no longer considered appropriate, because these two groups evolved from separate lineages.

### Microbial association with corals: holobiont

Corals exist as a community of multiple organisms that work together, termed the coral holobiont (Knowlton and Rohwer, 2003). These organisms include the coral animal, microbes, Fungi, endolithic algae, and zooxanthellae (Rohwer et al., 2002; Wegley et al., 2004). Microbes associated with corals are diverse, numerous and provide many functions (Kushmaro et al., 1996; Frias-Lopez et al., 2002). Microbes form species-specific associations (Rohwer et al., 2001); however, some taxonomic variation occurs between reefs (Littman et al., 2009).

### Functional role of microbes

Metagenomic analysis shows that microbes possess a gene complement that allows them to perform a diverse variety of functions (Wegley et al., 2007). Coral associated microbes have the genes to breakdown complex sugars and proteins, reflecting the types of carbohydrates excreted by the coral animal. Nitrogen fixation, ammonia assimilation, and nitrate/nitrite ammonification are functions that the coral associated microbes can conduct and these would enhance nitrogen recycling within the holobiont and potentially supplement supplies of nitrogen to the zooxanthellae. Coral associated microbes possessed multiple pathways involved in sulfur cycling. Microbes associated with Dimethylsulfoniopropionate (DMSP) breakdown are also common within the coral holobiont (Raina et al., 2009). Since sulfur is an essential element in the biosynthesis of amino acids, the microbial community may be playing a pivotal role in the coral growth. Other mutualistic benefits provided by the microbes include, the release of secondary metabolites, such as antibiotics (Castillo et al., 2001).

### Microbial role in coral stress

Changes in microbial complement associated with changes in environmental conditions may exacerbate coral stress. Corals exposed to four stressors, including increased organic carbon, inorganic nutrients, temperature, and

reduced pH, showed a variation in their associated microbial assemblage. Genes including those associated with virulence, stress response, sulfur and nitrogen metabolism, motility, and chemotaxis increased within the microbial community of stressed corals. The microbial taxonomic component associated with the stressed coral was dominated by species often associated with disease, including many *Bacteroidetes* and *Fusobacteria* (Vega Thurber et al., 2009).

### Microbial role in altering environmental conditions

Apart from symbiotic microbes, corals are influenced by the microbes present in their surroundings, such as those in the water column or in the substratum. Microbialization of the water column was a feature of coral reefs influenced by high levels of human activity (Dinsdale et al., 2008). On a coral reef with little to no fishing or human habitation microbial numbers were low and their gene complement matched that of a balanced autotrophic/heterotrophic community (Dinsdale et al., 2008). On reefs with higher levels of fishing and human population, microbes were highly abundant and dominated by heterotrophic microbes, many of which were similar to known pathogens. The increase in pathogenic-like microbes was correlated with an increase of unhealthy corals (Dinsdale et al., 2008; Sandin et al., 2008).

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## MID HOLOCENE

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### Definition

The Mid Holocene refers to a period of time between c. 7–5 ka cal BP during which large-scale ice sheet melt ceased. In regions far from former ice sheets, it was the first time in the present interglacial that relative sea level (RSL) reached or passed present levels. The end of ice sheet melt caused a change from rapidly rising RSL during the early Holocene (c. 10–7 ka cal BP) to relatively stable RSL between the mid Holocene and present.

### Introduction

The tropical reef environments of the Indo-Pacific and Atlantic have developed in different ways during the Holocene. This is due to the different broad-scale relative sea level (RSL) histories experienced by these two regions through time, particularly during and since the mid Holocene. It is important to understand how global sea level has fluctuated during this period in order to understand how these differences have come about.

The early Holocene period was characterized by a warming climate, which resulted in the complete melt of the Laurentide and Fennoscandinavian ice sheets, and a reduction in the size of the Greenland and Antarctic ice sheets. This large-scale ice sheet melt caused global sea level to rise quickly in far-field, low-latitude locations, which are distant from these ice sheets and are not affected by glacio-isostatic rebound. The rates of RSL rise in some far-field locations exceeded 8 mm/yr during the early Holocene (Sloss et al., 2007). By the mid Holocene, the majority of this melt had ceased; all North American and European ice sheets had disappeared, Antarctica was relatively stable, and the Greenland ice sheet had retreated inside its present margin.

Relative sea level in near and intermediate field locations record the effects of glacio-isostasy (see Chapter entries “*Glacio-Hydro Isostasy*” and “*Postglacial Transgression*”). However, these effects can extend to considerable distances, penetrating well into the tropical waters of the equatorial low latitudes. This is especially so for sites in the Atlantic Ocean which lie within the zone of influence of the former Laurentide Ice Sheet. It is therefore important not to assume that all tropical locations with fringing and barrier reefs lie in far-field locations and are unaffected by glacio-isostasy; tropical reefs in the Caribbean, for example, are not in the far-field zone, whereas the Indo-Pacific region is a genuinely far-field location.

### Equatorial ocean siphoning and continental levering

Results of a study combining glacio-isostatic modeling and RSL observations show that the Caribbean is located sufficiently close to the former Laurentide ice sheet to be on its lithospheric forebulge (Milne et al., 2005). The Laurentide ice sheet depressed the crust over North America and this caused displacement of the lithosphere away from the center of load. This caused a rim of crustal uplift outside of the depressed zone. When the ice sheet melted, the lithosphere migrated back to the former center of load and caused the forebulge to collapse. During the early Holocene, the effects of this process were masked by rapidly rising sea level caused by ice sheet melt, but since the mid Holocene this process can be seen in RSL records from both the forebulge region itself, and further away in the far-field.

In tectonically stable locations in the Caribbean, RSL has risen throughout the mid-late Holocene, despite the end of global ice melt c. 7–5 ka cal BP, because of direct crustal subsidence caused by forebulge collapse. In contrast, in the Indo-Pacific region RSL has fallen by a small amount (c. 1–2 m) in the late Holocene, as water has moved from the far-field regions back into space created by crustal subsidence in the forebulge region. This process is known as equatorial ocean siphoning (Mitrovica and Peltier, 1991).

A second process that may be as important as equatorial ocean siphoning in explaining late Holocene RSL fall in the Indo-Pacific region is continental levering. As the underwater shelves around continents were progressively flooded under rising sea level during the early Holocene, they subsided under the increased weight of water on them. Water from the center of large ocean basins (e.g. Indian and Pacific Oceans) flooded into the space created by these subsiding shelves, causing RSL to fall in the center of these ocean basins. Model results suggest that RSL fall in these locations comprises c. 60% due to forebulge collapse and 40% due to offshore subsidence around continental margins (Mitrovica and Milne, 2002).

### Effects on reef development

Reef development differences between the Caribbean (forebulge zone) and the Indo-Pacific (far-field), and within



the Indo-Pacific region itself (central ocean vs. continental margin sites), have been affected by the two processes described above. In the early Holocene, fast rising sea level in both regions provided accommodation space for reef growth, but after the mid Holocene (c. 7–5 ka cal BP) their broad histories diverge (see Chapter entries “*Holocene Reefs : Thickness and Characteristics*”, “*Sea Level Changes and Effects on Reef Growth*”, “*Reef Classification, Response to Sea Level Rise*,” and “*Reef structure*”).

### Caribbean model

Fast rising RSL in the early Holocene allowed high reef accretion rates, particularly in the Caribbean, where the average reef growth rate was c. 6 m/kyr (Dullo, 2005). Caribbean reef-building coral consists primarily of *Acropora cervicornis* (which grows in 5–15 m water depth) and *Acropora palmata* (which grows in <5 m water depth). Therefore, most Caribbean reef growth occurred after RSL rose to within 15 m of present (c. 9 ka cal BP) (Toscano and Macintyre, 2003). The exact timing of reef initiation depends on the depth of the antecedent surface, and can vary by c. 5 ka in locations with different reef-base elevations (Hopley et al., 2007). Caribbean reef-building corals were able to keep pace with RSL rise during the early Holocene (keep-up mode: Neumann and Macintyre, 1985), but as RSL slowed in the mid Holocene, back reef zones developed dominated by unconsolidated sand and rubble, representing a late succession stage of Caribbean reef development (Steneck et al., 1998; Gischler and Hudson, 2004). As RSL continued to rise at a slower rate in the late Holocene, *Acropora palmata* accretion continued to keep pace and slowly developed into framework-coral-covered reef flats.

### Indo-Pacific model

In the Indo-Pacific, RSL rose more rapidly in the early Holocene than in the Caribbean, although initial inundation of the –15 m contour occurred at about the same time (c. 9 ka cal BP: Pirazzoli, 1991). Unlike in the Caribbean, reef-building coral (*Acroporids* and *Poritids*) was unable to keep pace with RSL rise, entering instead a ‘catch-up’ mode where reef accretion lagged RSL rise (McLean and Woodroffe, 1994). As RSL rose to present in the mid Holocene, coral growth caught up with RSL, robust head corals with a dense framework were laid down, and an algal crust developed. The exact timing of reef attaining sea level is dictated by the depth of the antecedent surface and the amount of ‘catch-up’ it had to undergo, although this age range is much less than in the Caribbean because of the abrupt nature of RSL stabilization in the mid Holocene.

Under stable RSL from the mid Holocene onwards, tectonically stable locations saw lateral reef development as accommodation space for vertical reef growth disappeared. In many oceanic locations, this produced large reef flats and detrital carbonate platforms (Hopley, 1985). As RSL began to fall in the center of the Indo-Pacific ocean basins in the mid-late Holocene, these platforms became

emerged at low tide causing any coral living on them to die. There are many examples of coral microatolls from mid to late Holocene time stranded above their growth position on exposed reef flats in the Indo-Pacific region (e.g. Cocos Keeling Islands: Woodroffe, 2005).

These two idealized models of reef development under RSL rise assume no factors other than eustatic sea level affect reef growth. There are, however, some locations in the Indo-Pacific (e.g. Tahiti) where RSL has continued to rise through the Holocene and reef development has followed more closely the Caribbean than Indo-Pacific model. This is due to a variety of factors including volcanic and tectonic subsidence, which have caused continual, gradual submergence of Tahiti as it migrates away from a volcanic hotspot (see Chapter entry “*Volcanic loading and Isostasy*”). Similarly, in the Caribbean there are emerged mid Holocene corals on the island of Barbados, which are evidence of plate tectonic movement in this seismically active zone (Schellmann and Radtke, 2004).

While sea level was an important influence on the growth of coral reefs worldwide during the mid Holocene, other elements of the coral growth environment may also have been different to today’s. The period is often referred to as the Holocene Climatic Optimum and in the tropics much of the climatic data comes from the corals themselves (see Chapter entry “*Palaeoclimate from corals*”).

For many areas such as the Great Barrier Reef (GBR), a warmer climate of about 1.3°C, less variable wet seasons, fewer droughts, floods, and weaker ENSO events produced higher growth rates of individual corals (Gagan et al., 1998) and of coral reefs (see Hopley et al., 2007, ch. 11) within the period 8–7 ka which saw the most rapid reef growth on the GBR. Similar warmer, wetter conditions (from stronger monsoons) have been recorded elsewhere in the tropics in the mid Holocene (e.g. Gagan et al., 2000).

### Case study: the Great Barrier Reef

The GBR provides an example of how different types of reef morphology are dependent on different RSL conditions. The GBR shelf is wide (c. 230 km at its widest point) and has undergone differential movement through the Holocene. The offshore part of the shelf has subsided over time compared to the inner shelf due to hydro-isostatic loading, resulting in continuous RSL rise at the outer edge and a mid-late Holocene RSL fall on the inner part of the shelf (Nakada and Lambeck, 1989; Woodroffe, 2009). The reefs at the outer edge of the shelf are primarily made up of framework coral, most often found in keep-up situations, like those of the Caribbean. Inner shelf reefs, on the other hand, are described as ‘detrital piles with coral caps’ (Hopley et al., 2007, p. 390), with unconsolidated sediment increasing significantly across the shelf. Inner shelf reefs have also undergone emergence and erosion through the mid-late Holocene under slowly falling RSL.

Another factor affecting reef growth and morphology was the “mid *Holocene High Energy Window*” (see entry).

On the GBR, this existed between about 8 and 5.5 ka when outer reefs lagged behind those of the inner shelf (including fringing reefs) and did not protect the inner shelf reefs. Much of the carbonate productivity went into building coral shingle ridges on the shores of adjacent high islands. Subsequently, there has been a decline in both the rate of reef growth (including fringing reef progradation) and shingle ridge accumulation (Smithers et al., 2006).

### Summary/conclusions

Broadly speaking, reef accretion in both the Indo-Pacific and Caribbean regions is dominated by ice-sheet-melt-driven sea-level changes through the Holocene. Differences in reef morphology between the two regions, including the amount of framework coral and the extent of reef flats, reflect relatively small-scale variations in regional RSL, which occurred since the mid Holocene. These differences are due to long-lived global-scale isostatic processes which cause sea-floor subsidence (RSL rise) in some regions and RSL fall in others since the mid Holocene.

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### Cross-references

Glacio-Hydro Isostasy  
 Holocene High Energy Window  
 Holocene Reefs: Thickness and Characteristics  
 Paleoclimate from Corals  
 Postglacial Transgression  
 Reef Classification, Response to Sea Level Rise  
 Reef Structure  
 Sea Level Change and Its Effect on Reef Growth  
 Volcanic Loading and Isostasy

### MIDWAY ATOLL (HAWAIIAN ARCHIPELAGO)

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### Introduction

Midway Atoll is a subtropical reef near the northwestern end of the Hawaiian Archipelago at 28° 12' N and 177° 22' W, approximately 2,000 km from Honolulu and 259 km east of the International Date Line. Midway is an unincorporated U.S. territory and the only island in the archipelago not a part of the State of Hawai'i. It is second only to neighboring Kure Atoll, 60 km to the northeast, as the Pacific's most northerly atoll. Midway is roughly 9 km in diameter; 40 km<sup>2</sup> in total area; contains two main islands, Sand (1,200 ha) and Eastern (135 ha);



**Midway Atoll (Hawaiian Archipelago), Figure 1** Satellite view of Midway Atoll, showing Eastern and Sand Islands (southeast and south), the dredged channel through the perimeter reef (south), and the lagoon and pinnacle reefs (center). Source: Courtesy of Quickbird satellite imagery, 2007.

and one smaller islet, Spit Island (2 ha), (Figure 1). The atoll includes a large, shallow, triangular perimeter reef that encircles a mostly shallow lagoon (6,000 ha) with a maximum depth of 20 m. The perimeter has emergent reef along its northern sector. A similar emergent reef is also found along the northern rim of Kure Atoll suggesting a common origin.

### Geology

Midway was formed approximately 28 million years ago over the same volcanic hotspot that is now forming Hawai'i Island, the largest and south-easternmost island in the chain, 2,500 km southeast of Midway. Midway and Kure Atolls are at the northwest end of the Hawaiian Islands, and are among the six atolls, one low reef island, three high volcanic islands, and 30 submerged banks comprising the Northwestern Hawaiian Islands (Figure 2). Further to the northwest of Kure and Midway, the chain continues as a series of older drowned atolls and islands, called the Emperor Seamounts that extends to the Bering and Kamchatka Trenches off northern Siberia.

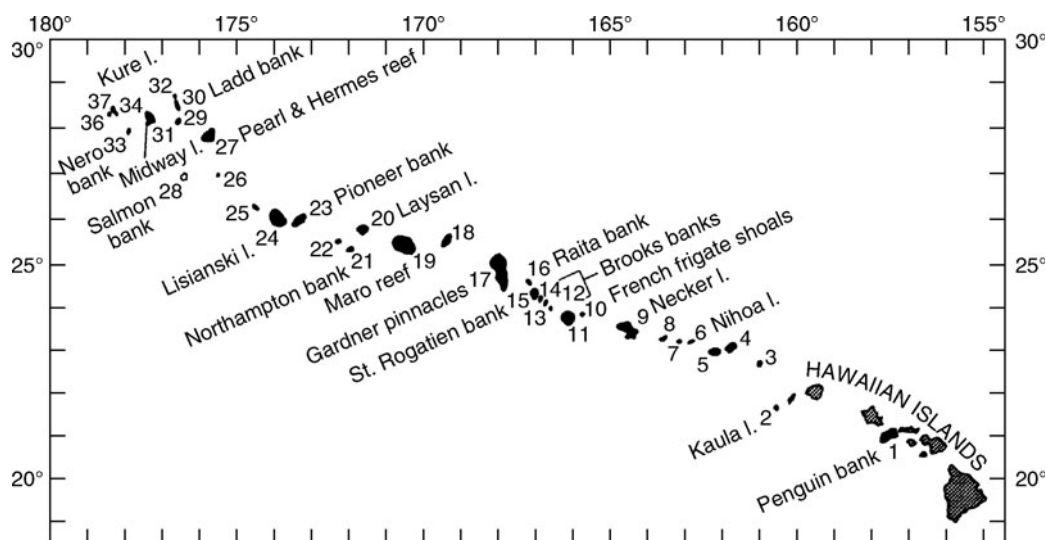
In 1965, the U.S. Geological Survey took vertical core samples at Midway and hit the solid basaltic rock formed by ancient volcanic eruptions at 55 m beneath Sand Island and 378 m beneath the reef at the northern edge of the lagoon (Figure 3). Core analyses of foraminifera and

limestone revealed a very complex evolution of reef and sediment deposits dating back to the Miocene that formed in shallow waters and providing evidence that the coral reefs have maintained upward growth as the atoll's volcanic base subsided. At least two Pleistocene unconformities were noted in upper layers, providing evidence of multiple episodes of sea level rise and fall. The thickness of the atoll's Holocene reef is approximately 160 m, and sediments in the lagoon are 384 m thick consisting of post Miocene deposits. Analysis of fossil corals in the core reveals that previous climatic conditions at Midway were more favorable for growth and abundance of corals. As with contemporary reefs at Midway, coralline algae were also dominant calcifying organisms.

### Human history

The first recorded landing at Midway Atoll was made in 1859 by Captain N.C. Brooks aboard the ship *Gambia*. In 1867, the Secretary of the Navy sent Captain Reynolds to take possession of the atoll for the United States. Efforts in 1871 to establish a settlement and open a channel through the perimeter reef failed, and for the next 30 years visits to the atoll were limited to shipwrecked survivors and bird hunters. Midway's role as an important communication link was established in 1903 when the Commercial Pacific Cable Company chose Sand Island for one of





**Midway Atoll (Hawaiian Archipelago), Figure 2** Map of the Hawaiian Islands archipelago with Midway near the northwest end and including all of the 37 submerged banks which are numbered. Source: Grigg and Epp (1989).

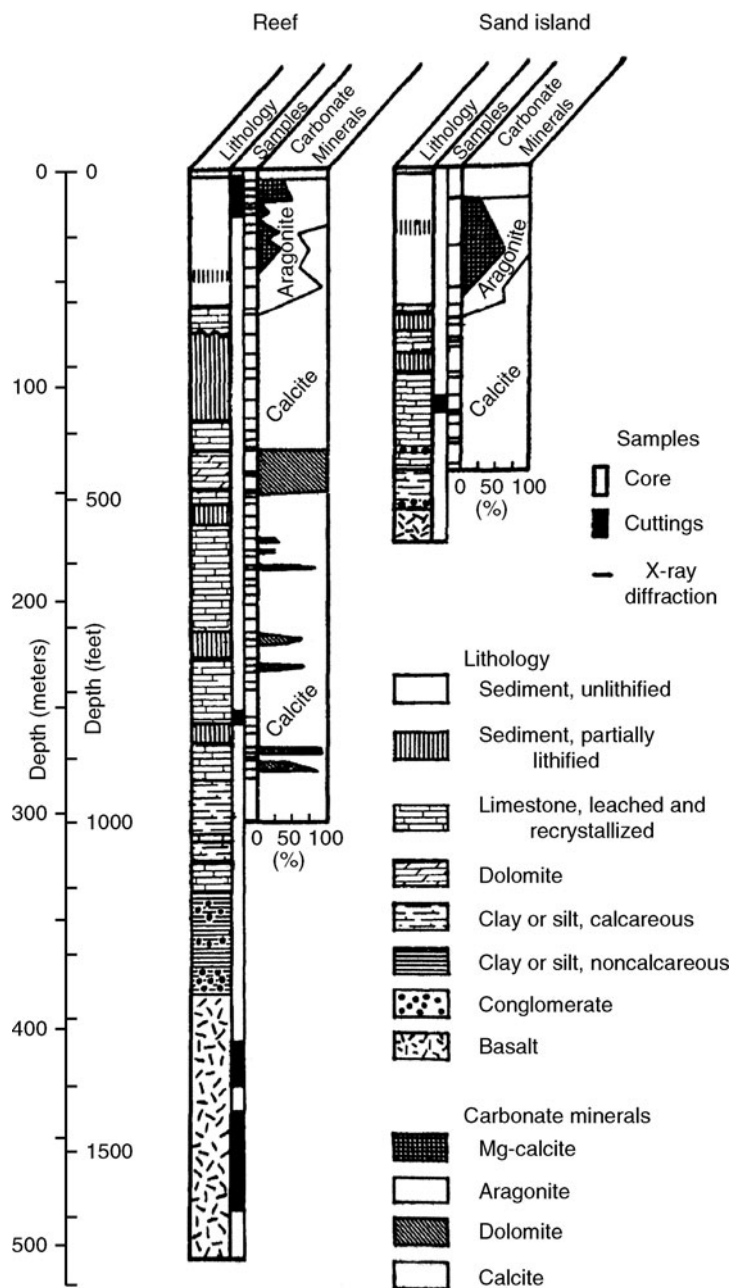
its relay stations. Cable Company employees reported foreigners landing at Midway, and especially disturbing were Japanese feather hunters who since the 1880s had decimated nesting seabird colonies. In January 1903, President Theodore Roosevelt placed the Midway Islands under the jurisdiction and control of the Navy Department to stop the “wanton destruction of birds that breed on Midway” and to establish a coaling station for Navy warships. In 1935, Pan American World Airways established a seaplane base in the harbor, including the clearing of some coral heads from the lagoon, and constructed a small luxury hotel on Sand Island. Midway became a regular refueling stop on a trans-Pacific route that also included Honolulu, Wake Island, Guam, and Manila. The short-lived era of the “flying clipper” seaplanes ended with the onset of World War II, and in early 1941, a U.S. Naval Air Station was commissioned on Midway. In the summer of 1941, 1,500 workers and a dozen dredges began excavation of the deep ship channel through the southern perimeter reef. “The big lagoon impounded incalculable tons of water coming in over the reefs, and poured it all out through the new channel in a current that often reached six miles per hour”, Woodbury (1946) reported. The dredging lowered lagoon water levels and exposed some of the perimeter back reefs. Likely changes in lagoon circulation included suspension of fine colloidal sediments accumulating on the lagoon floor caused by changes in deep water circulation patterns attributed to the new channel. On December 7, 1941, Japanese war planes bombed both Midway and Pearl Harbor.

Midway is well known for its role in the Battle of Midway. On June 3, 1942, a Japanese occupation fleet was spotted by a Midway patrol plane, and early on June 4, Japanese carriers launched three waves of planes to destroy the air base at Midway and clear the way for

occupation. Airplanes on both sides of the battle were lost, and extensive physical damage and casualties occurred on Sand and Eastern islands. From June 4–6, most of the battle was fought in open seas northwest of Midway. The Japanese Navy never fully recovered from the loss of all four of its carriers, 256 aircraft, and more than 400 of its best aircrew, and the battle terminated Japanese eastward expansion in the Pacific. The WWII facilities at Sand and Eastern Islands were listed on the National Register of Historic Places on May 28, 1987.

Midway continued to serve as a strategic location for the military after the war. During the Korean conflict, Midway served as a refueling station, and in the late 1950s “Cold War”, Midway was substantially upgraded and became a central location for the Distant Early Warning Line’s Pacific Barrier, extending from Midway to Adak, Alaska. During the Vietnam War, Midway was a main aircraft and ship refueling station and served as a listening post for foreign submarine activity. Midway was the site of the June 1969 meeting of President Thieu of the Republic of Vietnam and President Richard Nixon. In the waning years of the Cold War, Midway’s strategic importance as a military base diminished, but its unique historic associations and superb wildlife habitat quickly gained recognition.

An overlay refuge at Midway Atoll was established in 1988 when the U.S. Navy invited the U.S. Fish and Wildlife Service (FWS) to manage the atoll’s extensive wildlife resources. In 1992, the Department of Defense announced plans to close the Midway Naval Air Facility, and in 1996, the FWS assumed expanded jurisdiction over Midway after President Bill Clinton signed an Executive Order that transferred the atoll to the Service. Despite the efforts of Navy to clean up the atoll before transfer to the FWS, there are residual contaminated areas on the main islands where



**Midway Atoll (Hawaiian Archipelago), Figure 3** Preliminary logs of two 1965 Midway Atoll drill holes showing lithography, core recovery, and carbonate mineral composition of the cores. Source: Ladd et al. (1967).

soldiers defended the atoll during WWII, and where up to several thousand dependents, contractors, and soldiers lived and worked for more than half a century. Also, metallic debris remains in near shore waters as well as evidence of seeping contaminants and petroleum residues from the main islands.

The National Wildlife Refuge boundaries encompass “1,472 acres” of emergent land and “580,392 acres” of submerged lands and waters, out to “12 nautical miles”

(nmi). On June 15, 2006, President Bush added the Midway NWR in his Proclamation designating the NWHI Marine National Monument (MNM), and in 2007, its name was changed to the Papahānaumokuākea MNM. The Monument is managed by the NOAA, FWS, and the State of Hawai‘i, and it protects all 10 of the NWHI out to a distance of 50 nmi, including 30 submerged reefs inside the MNM boundaries. Midway is presently the only destination in the Monument open to public visitation.

## Marine species and habitats

Midway Atoll location in subtropical waters offers unique opportunities to study the effect of colder waters on the growth, development, and ecology of coral reefs. The atoll drops off steeply outside the perimeter reef, making it possible to observe within a relatively small area the different organisms and communities associated with pelagic, reef crest, ocean reef slope, deep reef, and lagoon habitats. The lagoon contains circular patch reefs in the deep central lagoon (Figure 1) and shallow back reefs near the lagoon perimeter. Both impede water circulation and trap sand washed over the reefs. These sediments limit coral development in much of the lagoon, except in the deeper central lagoon where stands of the endemic finger coral (*Porites compressa*) flourish. Corals are more abundant on some leeward ocean facing reefs and shallow back-reefs and lagoon pinnacles, but overall, corals are scarce on reefs exposed to ocean waves. A total of 33 species of stony corals and two non-stony corals (*Palythoa* and *Sinularia*) have been recorded at Midway, based on surveys from 2000–2006 and are dominated by *Pocillopora*, *Porites*, and *Montipora* species. These totals are slightly less than the 34–46 species found at the four nearest NWHI atolls and much less than the 66 species at the furthest atoll, French Frigate Shoals (FFS), 1,300 km to the southeast within the MNM. The close proximity of FFS to Johnston Atoll may facilitate dispersal of coral species between the Hawaiian and Line archipelagos and help explain the much higher species totals at FFS. The dominant blue encrusting coral at Midway is now tentatively identified as *Montipora dilatata*, an endemic species that displays spectacular formations in the lagoon and back reef habitats at Midway and several neighboring atolls, but which is rare in the larger MHI. Approximately 12 of the Midway coral species are endemic (~40%), an above-average level for the NWHI but comparable to the remaining NWHI.

In September 2002, marine biologists were surprised to find extensive bleaching of corals at Midway and two neighboring atolls (Kure and Pearl and Hermes) in these subtropical waters. Less severe bleaching occurred again at the same atolls during the late summer of 2004. Corals at Midway, where the 2002 bleaching was especially severe, must adapt to colder winter water temperatures of 18°C, as well as adapting to summer temperatures, normally 8–10 degrees higher. During the bleaching event of 2002, temperatures reached 29°C, 11° higher than the winter lows, and the corals responded by bleaching. Corals have recovered well during the past several years although there has been a net loss of lobe coral (*Porites*) compared to levels at permanent transects in the lagoon prior to the bleaching events at Midway.

Patches of the seagrass (*Halophila*) are reported in the lagoon, and calcareous green algae, brown turban algae, and crustose coralline algae are common on the outer reef crests. Large numbers of rock boring sea urchins (*Echinometra*, *Heterocentrotus*, and *Echinostrephus*) predominate, hollowing out the dead skeletal portions of live

lobe corals (*Porites*) and riddling the coralline algal covered reef crest with numerous holes and burrows. Scientists of the University of California at Santa Cruz are now determining whether reef erosion primarily from the boring urchins is outstripping reef growth, and whether selective removal of urchins would prevent serious erosion of the perimeter reef crests, the main natural barrier protecting the lagoon and islands. Beyond the reef massive spurs and grooves high in coralline algal cover face the open ocean along the northwest to southwest perimeter reefs, providing clear evidence of the importance of coralline algae as a major reef builder and bulwark in the far end of the NWHI. More than 100 species of algae are now known from Midway, including 35 new records for Midway and one species new to science, *Dudresnaya babbittiana*. A thorough 1997 survey reported no alien algal species at Midway. Quantitative surveys in 2006 revealed that *Lobophora*, *Laurencia*, *Microdictyon*, *Padina*, crustose coralline algae, and *Halimeda* in descending order were the most abundant algae at Midway.

The first systematic marine invertebrate survey was done at Midway in 1997. It documented 316 invertebrate species, 250 of which had not been previously recorded at Midway. Crustaceans dominated the larger invertebrate species, composing 46% of the total species. Other conspicuous marine invertebrates included sea urchins, with the burrowing sea urchin *Echinostrephus* responsible for the highest densities in the NWHI reported at Midway and Kure (>12 individuals/m<sup>2</sup>). The most common sea cucumber was *Actinopyga* and the most common sea star was *Linckia multifora*. The crown-of-thorns sea star, *Acanthaster planci*, has been reported at Midway at low levels. The black-lipped pearl oyster, *Pinctada margaritifera*, has also been recently reported at Midway.

A total of 258 species of fish, including 7 pelagic species, have been recorded on Midway reefs by 1993. Despite its low species diversity, Midway's reef fish biomass is higher than in the MHI, largely due to reduced fishing pressures attributed to the protective mandate of the NWR. Midway ranked fifth in terms of species richness, but ranked first in numerical density (2.7 individuals/m<sup>2</sup>), and ranked second in fish biomass, (2.5 t/ha) among all locations in the NWHI. Many Midway species grow to larger than average size, and all trophic levels are well represented, including jacks and four species of sharks. Some of these species are either not found on shallow reef habitats in the MHI or are very rare there. Several of these are limited to deep waters in the MHI, but are found at shallow diving depths (15–50 m) at Midway, including the only endemic Hawaiian grouper, the hapu'upu'u, (*Epinephelus quernus*) a species commercially harvested at greater depths (150–200 m) in the MHI, but fully protected within Midway NWR. This disparity in depth distribution is explained by the fish staying in the same isotherms extending upward to shallower depths at Midway compared to their greater depth regimes in the MHI.



Threatened green sea turtles are frequently seen inside the lagoon and basking on beaches, and 2007–2008 marked the first turtle nesting in many years. Endangered hawksbill sea turtles (*Eretmochelys imbricata*) are infrequently seen in the lagoon. About 65 endangered Hawaiian monk seals (*Monachus shauinlandsi*) are usually present at Midway at any time, and pup levels have increased significantly since the establishment of the NWR in 1996. Approximately 150–200 Hawaiian spinner dolphins use Midway's lagoon; bottlenose dolphins are commonly seen outside the reef; and striped dolphins, spotted dolphins, and rough-toothed dolphins have also been reported. Endangered humpback whales and other whales are also occasionally seen off Midway.

### Terrestrial wildlife and habitats

Humans have greatly changed Midway Atoll from its original form. The combined effects of dredging and filling, seawall construction, and importation of herbs and many plant species has greatly expanded the original acreage and made Midway a different place, but one that is still a wildlife habitat of worldwide importance. The earliest botanical descriptions of Midway were made in 1902, and since then more than 265 different terrestrial taxa have been identified. Nine of these are endemic to the NWHI and another 17 are indigenous to the HI. One endemic plant species, *Cenchrus agriminoides* var. *laysanensis*, is listed as endangered. Ecological restoration efforts are underway to eradicate invasive and noxious weeds, control others, and restore some habitats with native species. Since the first insect (a moth) was described from Midway in 1894, more than 300 species of arthropods and land snails have been found on Midway, mostly introduced aliens.

Almost two million breeding seabirds of 15 species make Midway one of the most important breeding areas of seabird conservation in the Pacific. Midway hosts the world's largest populations of both the Laysan albatross (396,936 nesting pairs) and black-footed albatross (23,963 nesting pairs) in 2009, accounting for 67 and 39% of the world's totals, respectively. One or two endangered short-tailed albatross generally visit Midway each year, but none have nested yet. Midway's breeding populations of white terns, black noddies, and red-tailed tropicbirds constitute the largest colonies in the Hawaiian archipelago. After eradication of rats in the mid-1990s, the Bonin petrel colony at Midway had rebounded to more than 32,000 pairs by 2005.

In 2004, 20 endangered Laysan Ducks, were transported to Midway from their only home at the time, Laysan Island, within the Hawaiian Islands National Wildlife Refuge (now also within the Papahānaumokuākea MNM). Biologists wanted to establish a second "insurance" population of this endemic duck once found throughout the Hawaiian Islands whose distribution had declined during the past two centuries to the single hyper-saline lake at Laysan Island. The ducks have adapted well to Sand Island, surprising biologists by breeding during their first year on Midway, with at least

10 ducklings surviving. An additional 22 ducks were transported to Midway in 2005, most of which were introduced to Eastern Island. Over the last several years there were declines due to disease, but duck populations have now rebounded to their highest levels at Midway. The atoll also serves as an over-wintering area for several arctic migrant shorebirds, including the globally rare Bristle-thighed curlew. Predator-free islands are required for this large but vulnerable shorebird because they become flightless during their winter molt. Many other migratory birds also visit Midway, some regularly and some rarely.

### Current investigations

The provisions of the MNM include the total ban of commercial fishing by 2011, control of access and introduction of alien species, and monitoring, safeguarding, and restoring the many endemic, threatened and endangered species that depend upon Midway and the other atolls and reefs within the MNM for their survival. A management plan for the Monument has been coordinated and approved, and a research plan will soon be completed.

Some research will be devoted to tracking and promoting recovery of depleted, endangered or threatened species as well as fish targeted by commercial fishers that will become fully protected in 2011. Because general visitation will be allowed only at Midway within the Monument, there will be considerable monitoring and controlling of visitors to prevent harm to fish and wildlife, collecting of fish and wildlife, preventing the introduction of invasive and alien species, and minimizing the effects of trash and pollution. Much of the Monument marine habitats including offshore habitats at Midway still remain relatively unexplored, and so some effort will be devoted to exploration for new species and habitats to determine which need to be afforded special status and additional protection. Research will also be conducted to learn more about how relatively pristine reefs function and what lessons can be learned from comparisons with the status of stressed reefs outside the Monument. In addition, research efforts will continue to determine whether reef growth at Midway is keeping pace with erosion and subsidence, and whether additional measures will help to reduce adverse effects, such as selective removal of the large populations of sea urchins that are now eroding key shallow reefs that serve as natural breakwaters for protecting the entire atoll.

Floating marine debris discarded or lost by distant fishing fleets in East Asia continues to accumulate regularly at Midway. Since 1996 when cleanup efforts were initiated, 42,821 kg has been removed from Midway which ranks fifth in total quantity removed. Evidence of increased accumulation rates on the shores and reefs of the NWHI may be attributed to the southward movement of the Subtropical Convergence Zone in the north central Pacific.

### Controversies and gaps in current knowledge

A review of the field methods supporting the Darwin Point hypothesis (Grigg, 1982) revealed it relied primarily on

limited sampling of one coral species, with little attention directed at crustose coralline algae that dominate shallow reefs at Kure, Midway, and neighboring islands and atolls. The hypothesis also relied on annual mean seawater temperatures and ignored seasonal fluctuations, especially at Kure, Midway, and Pearl and Hermes Atolls. Cooler winter temperatures are thought to reduce coral growth rates, but the summer temperatures are similar along the entire NWHI and high enough not to reduce coral growth rates. Moreover, the warmest summer temperatures that resulted in the coral bleaching events of 2002 and 2004 at the northernmost atolls may be caused by reduced mixing from weaker winds situated closer to the center of the North Pacific high pressure ridge and by decreased circulation within large shallow lagoons (Brainard et al., 2004). Regardless, the atolls have fully recovered from the earlier bleaching as documented by coral re-growth and recolonization of earlier bleached habitats.

Siciliano (2005) reexamined the Darwin Point hypothesis and reported that, although coral growth rates generally decline as a function of increasing latitude in the NWHI, as first suggested by Grigg (1982), this decrease is habitat-specific. Coral colonies found in protected habitats throughout the NWHI chain (back reef and lagoon habitats on the atolls; bays sheltered from wave action at the islands lacking lagoons) show comparable growth rates of corals regardless of latitude. This may be explained by the microclimatic conditions experienced by corals growing in the shallower, and often warmer lagoon and back reef habitats, where they are not closely related to offshore SST. Conversely, corals growing in exposed habitats throughout the NWHI (fore reef of atolls and reef islands), experience temperatures more akin to offshore SST conditions, and therefore may be more likely to correlate to regional SST gradients, such as decreasing SST with increasing latitude corresponding to decreasing growth rates.

However, the growth rates measured by Grigg (1982) may also be underestimated at Kure Atoll because of selective sampling. In his assessment of coral growth rate throughout the NWHI, Grigg (1982) sampled *Porites lobata* exclusively at 10 m depths at exposed southwest facing fore reefs. Inspection of *Porites* growth rates in three habitats at Kure Atoll (Table 1, from Siciliano, 2005) reveals that the fore reef has the lowest growth rate for this genus, among all sites sampled. There is strong

evidence of local upwelling off the southwest sides of the islands and atolls of the NWHI resulting in cooler waters. Therefore, exclusive sampling from this area is likely to underestimate average growth rates for the atoll as a whole. Even so, the Siciliano (2005) growth rates of *Porites* from the fore reef habitat (4.5 mm/yr) were still higher than those reported by Grigg for *Porites lobata* (3 mm/yr), even if the data comparisons excluded the faster growing, branching species such as *Porites compressa* which is present but not common on Kure's fore reef. However, additional encrusting and massive growth forms of *P. lobata* and *P. evermanni* were included in the 2005 study because they are important reef builders at Kure. Inspection of Table 4.6 also indicates that, if *Porites* growth rates were adjusted to reflect those of other reef-building corals in the fore reef habitat using Grigg's approach (i.e., by averaging the *Porites* growth rates with those of other reef-building genera), the corals' growth rate would increase to 0.8 mm/yr, rather than decrease as suggested by Grigg (1982) who reported an adjusted growth rate of 0.2 mm/yr for Kure Atoll, the basis for proposing the atoll as the Darwin Point. As a result, the latter data sets do not support the early findings of Grigg (1982).

## Summary and conclusions

Midway Atoll has experienced numerous changes over the past century but is now fully protected indefinitely. Adequate funding for management and restoration measures will contribute to the resilience and survival of the atoll, its habitats, vegetation, fish, and other wildlife. More importantly, Midway is now open again for public visitation that will serve to educate many people about the beauty and value of the Refuge and in turn, promote support and continued protection by future generations.

Factors not necessarily limited to latitude or mean annual SST may be responsible for determining the ultimate fate of Kure and Midway atolls and their coral reefs over geological time. These include anthropogenic impacts, excessive bio-erosion, bleaching events, size of the reef caps, duration of geological time in shallow water, geological instability leading to slumping and collapse of reefs, storms, ocean acidification, sea level rise, weather anomalies, and more rapid rates of subsidence as the atoll moves further away from the Hawaiian Rise into the deeper sea floor. More likely the Darwin Point, including its location, size, and validity will likely be further examined and perhaps revised. Alternatively, the Darwin Point theory may be better characterized as a dynamic concept or axiom rather than a defined point on earth, such as being at Kure or neighboring Midway. A spatially explicit alternative might be to restate it as a zone or gradient of approximately 2,000 km in length stretching from Kure and Midway atolls toward the southeast through the more than 30 drowning banks in the MNM to the islands of Kaua'i, O'ahu and Moloka'i where there are several neighboring submerged coral reefs and banks not presently keeping pace with sea level.

**Midway Atoll (Hawaiian Archipelago), Table 1** Mean linear growth rates (mm/yr) of the five main reef-building coral genera in three habitats at Kure Atoll. Source: (Siciliano, 2005)

| Genus              | Fore reef | Back reef | Lagoon |
|--------------------|-----------|-----------|--------|
| <i>Porites</i>     | 4.5       | 7.4       | 10.1   |
| <i>Pocillopora</i> | 16.9      | 17.2      | 16.9   |
| <i>Montipora</i>   | 1.0       | 1.0       | 1.22   |
| <i>Pavona</i>      | 16.3      | 7.6       | 6.3    |
| <i>Leptastrea</i>  | 2.0       | 2.2       | 2.4    |

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## Cross-references

[Algae, Coralline](#)  
[Atolls](#)  
[Banks Island: Frasnian \(Late Devonian\) Reefs In Northwestern Arctic Canada](#)  
[Bioerosion](#)  
[Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity](#)  
[Corals: Environmental Controls on Growth](#)  
[Darwin Point](#)  
[Hawaiian Emperor Volcanic Chain and Coral Reef History](#)  
[Sea Level Change and Its Effect on Reef Growth](#)

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## MINING/QUARRYING OF CORAL REEFS

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## Definition

The extraction of coral, either in the fossil or living form, for use generally in the construction trade. This is a widespread activity in the Indian Ocean in particular, which results in extensive damage to the three-dimensional structure of the reef and its inhabitants.



Recovery of damaged reefs may be very limited, particularly when surfaces are reduced to mobile rubble which inhibits successful coral colonization and growth.

### Background

Coral mining has caused extensive degradation of reefs in a number of countries, which include India, Maldives, Sri Lanka, Tanzania, and the Philippines (Brown, 1997a). The use of coral rock as a construction material in many countries in the central Indian Ocean has had a long history, particularly in the building of mosques, temples, and shrines. Early photographs taken by Agassiz in Malé in the Maldives in 1903 show houses constructed of coconut leaves and available timber, but by the mid-late twentieth century construction of houses, boundary walls, groynes, and breakwaters with coral blocks was commonplace (Brown, 1997b). At Mafia Island, in Tanzania two forms of coral were extracted in the early to late twentieth century for both local and commercial construction (Dulvy et al., 1995); these were fossilized limestone and living reef coral. In Sri Lanka, corals are primarily used in the construction industry for production of mortar and plaster with subsidiary uses as lime in soil improvement and in the ceramic and cement industry. In India, corals (coral fragments or 'challi' rather than coral 'stones') are also used for the production of lime with lime kilns in the Tuticorin area of southern India, exporting lime all over the country to meet the demands of paper and sugar industries, leather tanning and bleaching, mortar production, and white wash paint. Coral 'stones' extracted from areas such as the Gulf of Mannar, India, are used as building blocks or in road construction and as source material for house decorations. Similarly, in West Sumatra branching and massive corals are extracted to sell as decorative materials for house walls. In the offshore islands, it is estimated

that over 10–24 tons of shells and corals are collected from the reefs per year in an activity that involves ten people collecting once or twice a week (Tomascik et al., 1997).

While the construction industry is a major user of corals in the above-mentioned countries, it is clear that there is wide variation in the exploitation of specific coral products by different countries. These differences are reflected in the total harvest of coral products and also in the site and method of exploitation. In the mid-1990s, in Sri Lanka the greatest proportion of coral rock (42%) was derived from fossil reefs inshore, whereas live coral collection represented 12% and coral rubble (collected from the beach and reef flats) 30% of the total harvest. In India, the collection of coral fragments greatly exceeded the collection of coral 'stones' mainly because of its ease of collection and the reduced demand for the latter. Conversely, in the Maldives coral rock was much more important in the construction industry in the mid-1990s (Figure 1) than coral fragments, while in Tanzania both fossilized limestone and live coral were used in building work.

### Methods of coral extraction

Generally, all living coral is extracted from shallow waters on leeward reef flats and reef edges and in the Maldives from the coral rims of faroes or ring reefs in depths of approximately 2 m of water. The actual choice of sites is dependent on several factors, which include the prevailing weather conditions dictated by the monsoon in the Indian Ocean and the proximity of the final destination of the coral. Throughout South Asia, the manner of harvesting coral rock is very similar, involving manual collection with iron bars (Figure 2). Favored corals include the massive genera *Porites*, *Platygyra*, *Goniastrea*, *Favia*, and



Mining/Quarrying of Coral Reefs, Figure 1 Example of the use of coral rock in construction in the Maldives.



**Mining/Quarrying of Coral Reefs, Figure 2** Mining coral from shallow reef flats in the Maldives.

*Favites* as well as the branching genera *Acropora* and *Pocillopora* (Brown and Dunne, 1988). In the Maldives, the mining of coral rock is carried out by a specific group of islanders from Maamigili in Alifu Atoll working from local fishing craft or dhonis. Corals are broken up and transported to the destination and left for a period in the open for the action of sun and rain to clean the rock of its living inhabitants and leach out the salts (Figure 3). The coral is then broken up into irregularly shaped coral nodules which are the directly incorporated into the building trade. It is estimated that in the Maldives, up until 1988, at least 200 m<sup>3</sup> of coral rock had been removed from reefs in North Male Atoll for use in the construction industry (Brown and Dunne, 1988).

### Biological effects of coral mining

Very similar biological effects of mining were found in two studies, one in the Maldives (Brown and Dunne, 1988; Dawson-Shepherd et al., 1992) and another in Tanzania (Dulvy et al., 1995). The effects included a marked decrease in coral cover and a lack of coral recovery on mined areas several years after coral extraction had ceased and also a reduction in overall abundance and diversity of fish communities across planktivorous, benthic herbivorous, and omnivorous trophic groupings (Brown and Dunne, 1988; Dawson-Shepherd et al., 1992; Dulvy et al., 1995). A loss of rugosity was also noted on mined reefs in the Maldives (Dawson-Shepherd et al., 1992). Butterfly fish or Chaetodontidae, which rely on corals as a source of food, showed marked reductions on mined sites in Tanzania, while in the Maldives, species such as the damselfish *Chromis* spp. were conspicuously absent from mined areas, probably because they depend on the three-dimensional structure of the reef for shelter and also on a pelagic supply of food. One reason for the

poor recovery of these mined reefs lies in the unstable nature of the resulting substrate, which by its mobile nature prevents successful colonization and growth of juvenile corals (Brown and Dunne, 1988; Clark and Edwards, 1994).

### Alternative management options and restoration of mined reefs

A number of alternative management options have been put forward to reduce demand for coral rock in the Maldives, which range from the use of concrete blocks (Figure 4) instead of coral rock to the commercial mining of a single faro reef (Brown and Dunne, 1988, 1995). In Mafia Island, Tanzania, the use of sun-dried mud blocks has been suggested as a replacement for coral products (Dulvy et al., 1995; McClanahan et al., 2000). Stricter legislation has also restricted the amount of coral mined in countries such as the Maldives (Brown, 1977b; Sluka and Miller, 1998), while participatory, collaborative management processes have had some success in Sri Lanka (Brown, 1997b) and Tanzania (McClanahan et al., 2000).

The use of artificial reef structures (concrete blocks and mats or chain link fencing and paving slabs) to promote reef growth on mined reefs is extremely costly but effective (Clark and Edwards, 1994) and while transplantation of corals from elsewhere to such structures has had some success, it is suggested that transplantation should only be undertaken if natural recruitment does not occur (Clark and Edwards, 1995; Edwards and Clark, 1998). The latter authors conclude that where suitable surfaces for settlement are available and water quality is conducive to coral growth, natural recruitment can provide significant restoration within 3–4 years. In the Maldives, stabilizing the substrate with concrete mats has encouraged successful coral recruitment on mined substrates.





Mining/Quarrying of Coral Reefs, Figure 3 Weathering of coral rock prior to its use in construction in the Maldives.



Mining/Quarrying of Coral Reefs, Figure 4 The use of concrete blocks in construction in the Maldives.

### Summary

There is no doubt that coral mining is still carried out within the Indian Ocean but because of legislation and the adoption of more sustainable alternatives, the quantities of corals mined today are much more limited than they were 20 years ago.

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## Cross-references

[Coral Reefs of India](#)  
[Maldives](#)  
[Reef Restoration](#)

## MOATING

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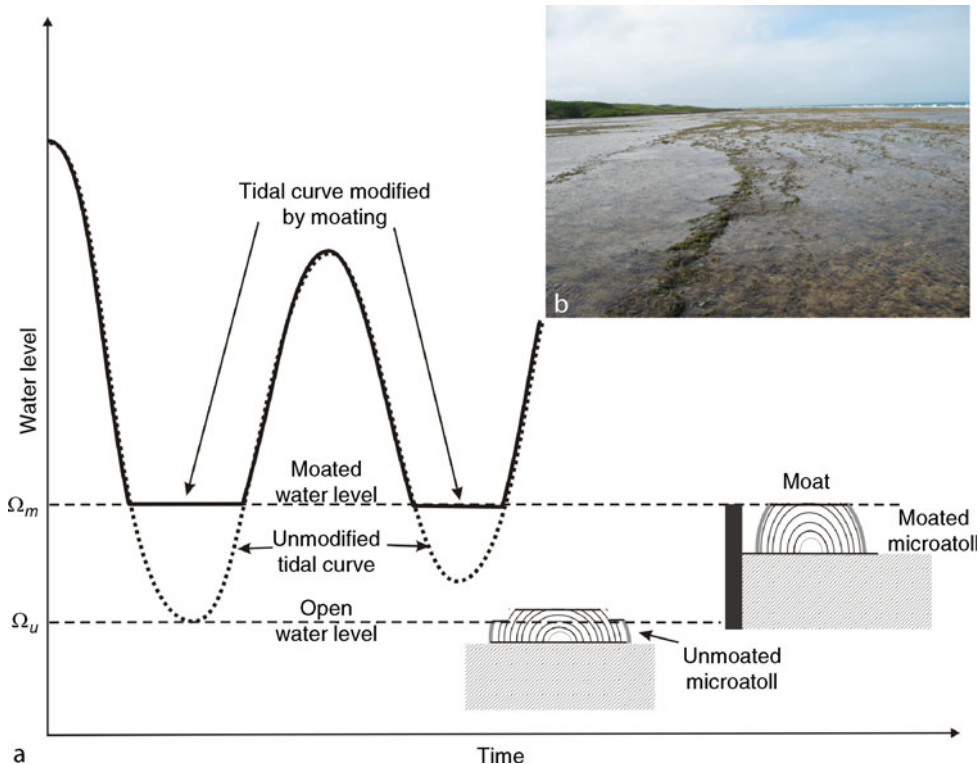
### Definition

Moating is the process of constraining the ebbing tide over the reef to produce moats in which low tide water levels remain perched above open water levels (see [Moats](#)).

Moating truncates the lower part of each tidal cycle at an elevation determined by the height (in the tidal frame) and permeability of the moating structure ([Figure 1a](#)). Moating can occur at any intertidal elevation and may only be active during the lowest spring tides.

Where moating occurs behind stable and impervious features, like algal rims (see [Algal rims](#)) the water level is consistent on every (lower) low tide. In contrast, at mesotidal locations like the central Great Barrier Reef (GBR) open water spring and neap low tides can differ by > 2 m.

Moating allows some reef biota to survive above their open water limits, and must be considered when



**Moating, Figure 1** (a) shows how moating above the low tide level, modifies the tidal curve and allows intertidal biota to survive above their open water limits. Moating occurs behind structures like these algal terraces on the reef flat at Bewick Island, northern GBR (b).

interpreting intertidal sea-level indicators, especially coral microatolls (see [Microatoll](#)) ([Figure 1a](#)). Moating also has important implications for sedimentation on reefs. It controls the tidal windows when tidal currents are active, and modifies reef flat depths and thus where reef top waves may entrain and transport sediments.

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Hopley, D., 1982. *The Geomorphology of the Great Barrier Reef: Quaternary Development of Coral Reefs*. New York: Wiley.

## Cross-references

[Algal Rims](#)  
[Great Barrier Reef Committee](#)  
[Microatoll](#)  
[Moats](#)  
[Reef Flats](#)

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## MOATS

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## Synonyms

Ponds; Reef top pools

## Definition

Moats are areas of water held over intertidal reef surfaces above the open ocean level during lower tides. Moats form when ebb-tide drainage is impeded behind biologically constructed or sedimentary structures. The former includes reef crest algal rims and algal terraces. Sedimentary structures include storm ridges or ramparts (commonly of coral shingle) and minor ridges of sand and gravel. Shallow moats may also pool in subtle reef flat depressions.

Moats behind algal rims can be impressive, impounding water well above the ocean tide, especially in areas of high tidal range. For example, a high algal rim extending > 2 m above the MLWS tide level encircles Redbill Reef on the central Great Barrier Reef, and holds water just 8 cm below MSL during low tides (Hopley, 1982). Moats of this type may cover several km<sup>2</sup>. Smaller algal terraces are common on the seaward slopes of algal rims and form shallower (< 20 cm) moated ponds typically 1–100 m<sup>2</sup> in size.

Moats confined by sedimentary structures may be less permanent in their construction and effect. For example, unconsolidated rubble and shingle ramparts tend to leak initially and are vulnerable to reworking. Although water remains moated above open water, small breaches can episodically lower water levels. Over time compaction, infill of voids with finer sediments, and basal cementation may improve the damming efficiency of these structures, but usually at a lower height than immediately post-emplacement.

Moats occur on most reef flats but are best developed where the tidal range is large, algal rims thrive, and coral growth and storm frequency provide enough rubble and depositional events. Emergent back reef, as produced by late Holocene relative sea level fall, is also excellent substrate for moat development.

Moats are important habitats that may support a diverse reef flora and fauna above the ocean low tide level. Moderately sized and cemented/encrusted moats are more physically stable and typically harbour the most diverse communities, especially where moat water is well flushed daily. Small shallow moats tend to be less permanent, and are vulnerable to biologically limiting thermal and salinity extremes.

Several other features are referred to as moats with varying degrees of correctness. Moated boat channels – containing water of navigable depth – occur on some reef flats, either immediately behind algal rims where surging waves and sediment flux limit reef growth or, on fringing reefs, nearer to the shore where terrestrial runoff achieves the same effect. Although in each case water may moat behind the algal rim, the deeper water is chiefly a function of locally restricted vertical accretion rather than ponding over the reef flat. Maldivian cay shorelines oscillate with monsoonal reversals and similarly constrain upward reef growth near the cay below that of the reef edge. The deeper zone separating the reef rim and cay formed by this process has also been called a moat.

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Hopley, D., 1982. *The Geomorphology of the Great Barrier Reef: Quaternary Development of Coral Reefs*. New York: Wiley.

## Cross-references

[Algal Rims](#)  
[Boat Channel](#)  
[Fringing Reefs](#)  
[Maldives](#)  
[Moating](#)  
[Reef Flats](#)  
[Shingle Ridges](#)

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## MOLLUSCS

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## Definition

The Mollusca are soft-bodied animals that usually have a hard, protective shell. They constitute the most diverse marine phylum and the most diverse group of coral-reef organisms (Paulay, 1997). Coral reefs provide substrata, protection, and food for molluscs (Caterall, 1998; Morton, 1983). In turn, molluscs influence reef growth and internal biological processes. Some gastropods prey directly on live coral tissue, causing, in some cases, a significant

impact in structuring of reef communities. Bioerosion of live coral skeletons and coral rock alters and destroys, ultimately reducing them to fine, unconsolidated sediments. Bioeroders may be divided into the epilithic and the endolithic (Glynn, 1997). Using their reinforced radular teeth, epilithic bioeroders abrade limestone in the process of grazing on algae or other organisms. These include chitons, patellids, trochids, littorinids, and neritids (Glynn, 1997). Endolithic bioeroders bore into coral skeletons using chemical and/or mechanical processes. Bivalves in the genera *Lithophaga*, *Gastrochaena*, *Fungiacava*, and *Choristodon* are active borers, whereas *Tridacna* and *Hippopus* show a limited degree of downward penetration (Glynn, 1997; Morton, 1983). Reef-building vermetid gastropods in the genera *Vermetus* and *Dendropoma* can be important contributors to the structure of coral reefs.

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## Cross-references

Bioerosion  
Sediment Dynamics  
Sediments, Properties

## MURUROA ATOLL

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## Definition

The atoll of Mururoa, also known as Moruroa or Aopuni, lies in the south-eastern end of the Tuamotu Island Group (21°50'S, 138°53'W) in the central Pacific. Politically speaking, this island is part of the French Polynesia.

## Geological setting

Mururoa is 28 km long and 11 km wide with a reef rim not exceeding 15 km<sup>2</sup> in surface area. It falls into the open-atoll type with a large natural pass (4,500 km wide, 1–9 m deep) on its leeward side. Its volcanic basement has originated from the Pitcairn hotspot at present operating about 70 km to the south-east of Pitcairn Island (Gillot et al., 1992). The cessation of volcanic activity

from about 11 to 10.5 million years favored prominent reef building. Subsidence of the volcanic shield at an average rate of 7–8 mm per millennium has been accompanied by deposition of a sedimentary pile varying between 130 and 570 m thickness (Buigues, 1997). From the end of the 1960s, in relation to nuclear testing, intensive biological, geological, and geophysical surveys were carried out on the modern reef and its carbonate foundations.

## Modern reef morphology and zonation

The reef zonation, the composition and distribution of major reef-building biological assemblages have been described by Chevalier et al. (1969), Bablet et al. (1995) and Camoin et al. (2001). Up to 50 coral species have been described from the fore-reef to lagoonal areas.

### The outer reef rim

The reef rim, 3 m in maximum elevation, consists of successive islets (« motus ») that form a continuous 400-m wide line along the windward side, and a discontinuous line, 1,100 m wide on the leeward side. The rim is made up of coral rubble mixed with skeletal sand, locally resting on the modern reef flat or overlying emergent, firmly cemented coral conglomerates of mid-to late Holocene age. The reef-flat zone is subdivided into three subzones. The outermost subzone is a typical algal ridge, up to 0.50 m high, 20–50 m wide, mostly made up of coralline algal crusts (*Hydrolithon onkodes*, *Chevaliericrusta polynesiae*) associated with encrusting foraminifera (*Homotrema*, *Acervulina*) and scarce robust branching corals (*Acropora humilis*, *Pocillopora verrucosa*). Behind the algal ridge, there is a coral-dominated subzone inhabited by stunted branching, massive, and encrusting colonies (*A. humilis* group, *Pocillopora brevicornis*, *Favia stelligera*, *Montipora caliculata*, *Porites lichen*). Behind the islets to the lagoon, there is an inner reef-flat subzone mainly covered by loose detritus and a few corals (*Acropora muricata*, *A. corymbosa*, *A. microphthalma*, *A. tenuis*, and *Alveopora allingi*).

The fore-reef zone can be delineated into three subzones. The upper subzone (to about 10 m deep) is gently dipping (less than 15°) and dominantly colonized by robust branching and massive corals (*Acropora robusta* group, *A. humilis* group, *P. verrucosa*, *P. eydouxi*, *F. stelligera*, *Platygyra daedalea*). Between the depth of 10 and 40–50 m, the intermediate fore-reef subzone becomes increasingly steeper (30–45°). The coral cover rate decreases; the dominating coral species include *Acropora nasuta*, *Astreopora myriophthalma*, *Leptastrea transversa*, *Echinopora gemmacea*, *Leptoria phrygia*, *Pocillopora elegans*, together with *Montipora* and *Cyphastrea*. The lower fore-reef subzone below 40–50 m forms a sub-vertical drop-off, locally covered by encrusting, tabular, and foliaceous corals (agariciids mainly) associated with coralline algae and encrusting foraminifera (acervulinids). In addition, the fore-reef zone exhibits terraces at 10, 20, 40, 55, and 65 m and cave-like



features at 80, 90, 100, and 150 m deep (Buigues, 1997). The terraces were interpreted as former tops of successive reef units deposited during the late Pliocene and the Pleistocene, while the caves may have been the result of dissolution controlled by colder, interstitial reef waters or by meteoric waters during former low sea stands.

Locally, brackish ponds form in shallow reef-rim depressions (Trichet, 1969) and contain cyanobacterial communities. These develop as mats (matolites or « kopara » according to Défarge et al., 1994) in which calcareous microbialites and phosphorites are deposited (see Richert et al., 2006 for review). These processes are thought to be promoted by nutrient-rich, thermally driven convective currents within the carbonate pile (i.e., the endo-upwelling concept of Rougerie and Wauthy, 1993).

### The lagoon

It averages 30–40 m depth and contains numerous reef patches. Coral communities on both lagoonal floor and patches consist chiefly of arborescent *A. muricata* group, *A. pulchra*, massive *Porites lobata*, *Leptastrea purpurea*, *Favia speciosa*, and branching *P. verrucosa*.

### Lithology and structure of the sedimentary pile

During the building of the volcanic shield, submarine eruptive events close to the sea surface have alternated with episodes of coral settlement, resulting in coral-rich layers embedded into the volcanic rocks. The deepest occurrence of carbonate deposits is about 950 m beneath the modern rim surface. The volcanic rocks are overlain by a sedimentary pile that comprises two distinct series: a basal volcanoclastic series and a carbonate cap. The entire pile displays a number of seismic reflectors identified in cores as unconformity surfaces at the top of different diagenetic units (Buigues, 1997).

### The volcanoclastic series

It ranges between 100 and 0 m in thickness from the periphery to the center of the atoll. The series is typified by the superimposition of transgressive (retrograding) depositional sequences. At base the sequences are usually composed of volcanic conglomerates. Progressively upwards, the volcanoclastics decrease in grain size and thickness to thin sand beds. Correlatively, coral-derived material increases in volume, locally forming massive buildups trapped into the volcanoclastics. The younger volcanoclastics are found at around 300 m below the modern reef rim.

### The carbonate cap

It occurs between 300–500 and 120–220 m beneath the reef rim and the center of the atoll respectively. An array of reef-related facies has been identified and includes corallgal framstones and bindstones, with skeletal rudstones to grainstones typical of high-energy, outer rim environments; coral bafflestones associated with skeletal

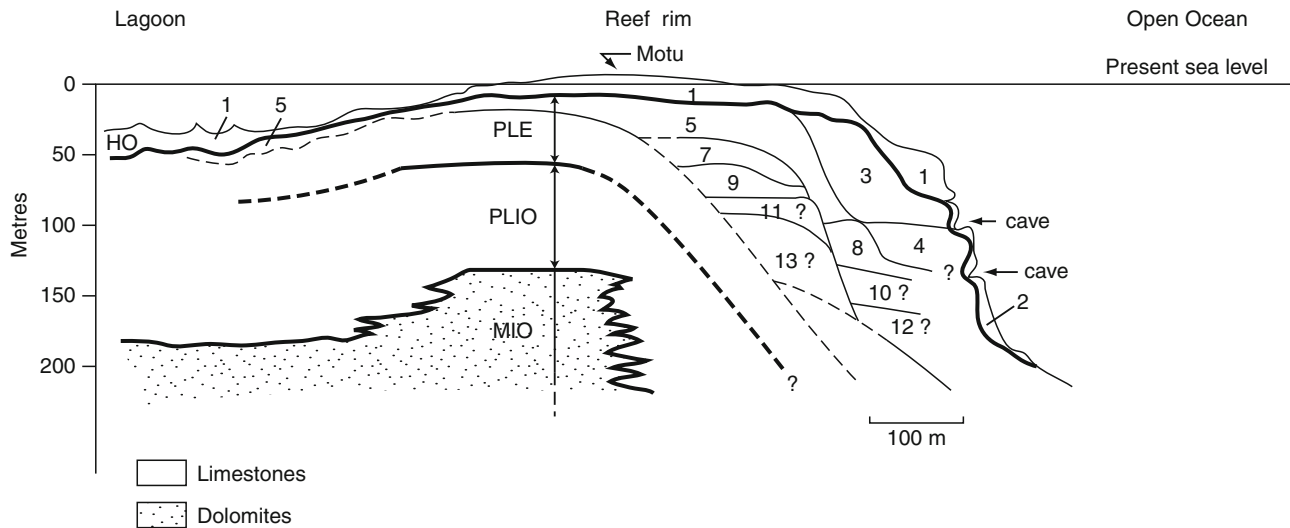
floatstones to wackestones, characteristic of low-energy environments; coral platstones to sheetstones embedded into wackestones to mudstones, typical of sheltered, lagoon-like environments. The spatial distribution of these facies reveals that the carbonate system has evolved in terms of morphology and architecture over time. The development history of the carbonate cap has been reconstructed on the basis of age determinations, i.e., radiocarbon, uranium-series, and magnetostratigraphy (Buigues, 1997). The settlement of fringing and barrier reefs is likely to have been discontinuous throughout the Miocene, primarily controlled by volcanic activity and, from about 10.5 million years by residual volcanic topography, tectonics, and sea-level changes. The entire volcanic basement has been capped by an extensive flat-topped carbonate platform probably not prior to the Pliocene. The classical atoll morphology is thought to have been acquired during the late Pliocene to Pleistocene. This results from both dissolution in the central platform areas and lateral reef accretion at the periphery in response to changes in sea level (Perrin, 1990; Buigues, 1997; Camoin et al., 2001). From top to base, the carbonate cap is composed of four stratigraphical units. The Holocene reef unit ranges between about 4 and 20 m in thickness. The Pleistocene reef unit is about 50–150 m thick. It displays major unconformity surfaces at 10, 30, 65, 80, and 90 m below present reef surface, separating successive reef generations. The Pliocene reef unit ranges from about 70 to up to 150 m in thickness. The oldest unit (Late Miocene) locally exceeds 150 m in thickness (Figure 1).

### Carbonate diagenesis

The carbonate rocks from both the volcanoclastic series and carbonate cap have suffered severe diagenetic alteration (replacement by low-magnesium calcite and dolomite, dissolution, karstification) probably controlled by freshwater aquifers in relation to changes in sea level (Aissaoui et al., 1986). There is a significant increase especially, both in calcite and dolomite diagenesis towards the periphery of the carbonate cap. Apart from the upper 20 m (Holocene) composed of metastable minerals (aragonite, high-magnesium calcite), the cap contains low-magnesium calcite or dolomite. The dolomite unit probably of late Miocene Age, occupies the lower two-thirds of the carbonate cap (Figure 1). Dissolution is one of the most prominent diagenetic features in the carbonate cap. The whole series appears to be severely karstified. Karst starts at 90–100 m and extends down to 150 m within the Pleistocene carbonates, both beneath the rim and the lagoon. Large-scale karstic surfaces also occur 180–200 m deep at the Pliocene–Miocene transition and 220–280 m and 300–350 m deep at the base of the Miocene carbonates.

### Pleistocene reef growth and sea-level changes

Uranium-series age determinations of the successive reefs units drilled through the outer rim at Mururoa provide new



**Mururoa Atoll, Figure 1** Lithology and structure of the carbonate cap with special reference to the outer reef rim over the last 300 ka, Mururoa Atoll, French Polynesia. *HO* Holocene unit, *PLE* Pleistocene unit, *PLIO* Pliocene unit, *MIO* Miocene unit. Numbers 1–12 refer to Marine Isotope Stages (MIS). Modified from Buigues (1997) and Camoin et al. (2001).

constraints on reef physiography and variations in sea level during the past 300 ka (1 ka = 1,000 years) (Perrin, 1990; Camoin et al., 2001). The outer rim has developed seawards in the form of a series of overlapping fringing reefs (Figure 1). Estimates of former sea-levels are based on the age-depth relationship of selected corals with correction of the present depth for both thermal subsidence of the atoll and habitat-depth range of the corals. Prominent reef units primarily made up of corallgal boundstones have developed during four episodes of high sea stands (MIS stages 1, 5, 7, and 9). The data indicate that sea level was between 17 and 23 m below present sea level (bpsl) at 9 ka. During MIS stage 5 e (around 125 ka), sea level is estimated to have been 6–10 m above present reef surface. The paleo-sea levels at 212 ka (stage 7 c) and 332 ka (stage 9 c) were 11–17 m 26–33 m bpsl respectively. Low sea stands are typified by limited reef growth and large skeletal deposition and include MIS stages 2, 4, and 8. During stage 2 (Last Glacial Maximum), sea level was around 135–140 m bpsl within the 23–17 ka interval. The paleo-sea level during stage 4 at around 60 ka is assumed to have been between 76 and 91 m bpsl, while it was at 79–94 m bpsl during stage 8 d at about 270 ka.

## Summary

Mururoa is an open atoll and exhibits low coral diversity (about 50 species). Drilling investigations revealed that the maximal thickness of the carbonate pile ranges between 500 and 220 m. The lowermost part of the pile is late Miocene in age. The typical atoll morphology is likely to have been acquired not before the late Pliocene. During the Pleistocene, and especially the last 300 ka, the outer rim has accreted seawards through a series of

stacked fringing-like reef bodies. The carbonate deposits have experienced intense diagenetic alteration by fresh water during successive low sea stands.

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## NEW CALEDONIA

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### Introduction

New Caledonia is located in the South West Pacific Ocean and comprises several islands and islets and a broad diversity of oceanic and continental reef structures including (non-exhaustive list) shoals, atolls, uplifted reefs, drowned reefs, patch reefs, fringing reefs, and barrier reefs (Andréfouët et al., 2009). In the recent review by Andréfouët et al. (2009), the mapping by high spatial resolution optical remote sensing data indicated that the 161 unit types of the New Caledonian coral reef complexes were distributed across 4,537 km<sup>2</sup> of reef area and 31,336 km<sup>2</sup> of non-reef area. More specifically, between the coastlines of the main island, called the Grande Terre, and the barrier reef, a more or less wide lagoon of approximately 30 m depth extends along both sides. The Grande Terre is bordered along the 500-km-long coastline by one of the longest barrier reefs in the world (1,600 km), double or triple in several parts (Guilcher, 1988), interrupted by passes, often in front of rivers, and by drowned segments, especially along the east coast. This barrier reef extends northward, enclosing the North lagoon and the Belep islands; it also extends southward, enclosing the south-west lagoon or lagoon of Nouméa enclosing several coral islets and the Ile des Pins (Figure 1). The coastlines of the Grande Terre are bordered by fringing reefs particularly well developed on the east coasts while mangroves alternate with fringing reefs on the west. For instance, our knowledge on the development and history of coral reefs in New Caledonia is focused on the Grande Terre and

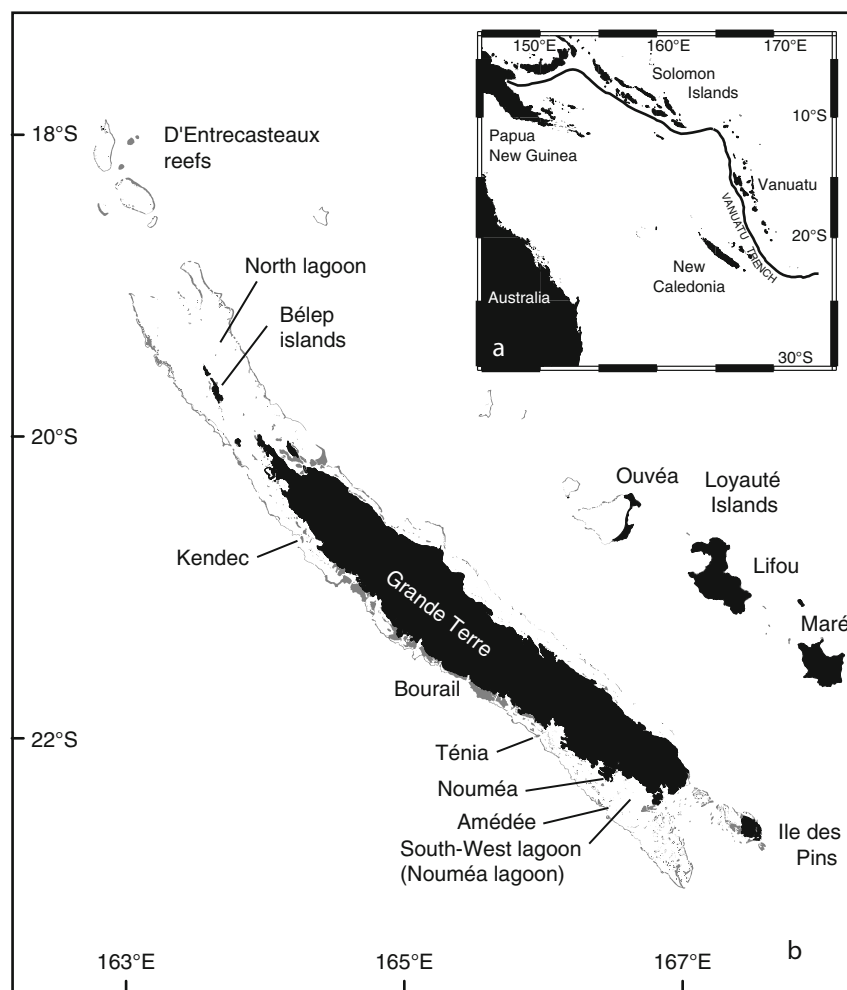
Loyauté islands. Little is known regarding the reef evolution of the shoals, atolls, and drowned reefs.

### Climatic conditions

Two marked seasons can be reported: (1) from November to April during the austral summer, the climate is tempered by the prevailing southeast trade winds and (2) from May to October, during the austral winter, the trade winds are disturbed by westerlies generated by polar air masses. Moreover, New Caledonia can be affected by tropical cyclones from November to May with some damages to reefs as recently reported (Guillemot et al., 2010). Due to its location, New Caledonia is in the south of the West Pacific Warm Pool (WPWP) under the influence of the interannual climatic variations resulting from the El Niño Southern Oscillation (ENSO) phenomenon. In this region, the fluctuation of the south branch of the Intertropical Convergence Zone (ITCZ), the South Pacific Convergence Zone (SPCZ), is marked by variations in the oceanographic parameters. During the “La Niña” events, New Caledonia experiences high rainfall and variations in sea surface salinities (SSS) (Delcroix and Lenormand, 1997). During the last decades, ENSO events and climatic variability were investigated using analyses of isotopes ( $\delta^{18}\text{O}$ ) and trace elements (Sr/Ca, U/Ca, Ba/Ca) at a monthly resolution on corals, to reconstruct the past sea surface temperatures (SST), SSS and nutrient inputs (Beck et al., 1992; Quinn et al., 1996, 1998; Corrège et al., 2001; Stephans et al., 2004; Ourbak et al., 2006; Delong et al., 2007).

### Geological setting

New Caledonia is located on the Australian tectonic plate, which dips beneath the North Fiji Basin microplates and Pacific tectonic plate. The subduction zone (Vanuatu trench) is situated eastward of the Loyauté islands (Figure 1). The resulting deformation of the Australian



**New Caledonia, Figure 1** (a) The south west Pacific showing the plate boundary and the location of New Caledonia, Vanuatu archipelago, Solomon islands, Papua New Guinea, and Australia. (b) The mainland of the Grande Terre of New Caledonia, the Loyauté islands, "île des Pins," and the d'Entrecasteaux reefs (modified after Cabioch et al., 1996). The coral reef line is reported from Andréfouët et al. (2009).

plate, the lithospheric bulge, can be observed in the variations of altitude of the uplifted atolls of the Loyauté islands (Dubois et al., 1974, 1975; Guyomard et al., 1996). Globally, it appears that the morphology and the distribution of coral reefs in New Caledonia highly depend on the vertical motions (Chevalier, 1968; Cabioch et al., 1996) so that their morphological studies and the coral datation provide data on the neotectonics in the Late Quaternary. In this way, the study of the variations in depth or altitude of the 125 ka (1 ka = 1,000 years) reefs (generally expected at +6 m above the modern sea surface) and the modern reefs documents on the differential vertical movements and the recent motion rates. The overall setting of the 125 ka reef around New Caledonia shows an irregular increasing island subsidence tendency northward and southwestward from a relatively more or less central zone (Cabioch et al., 1996). For instance, Frank et al. (2006) show that the Amédée reef, in the southwest (Figure 1),

subsided at a rate of at least  $0.16 \text{ mm y}^{-1}$ , while the reefs close to the coast, for example, as at Nouméa, subsided at  $0.07 \text{ mm y}^{-1}$ . Subsidence is also low,  $0.03 \text{ mm y}^{-1}$ , near Bourail in the West. It appears that the highest subsidence rates were observed offshore explaining the formation of the wide southwest and North lagoons. The modern coral reef growth and reef morphology are also affected by the hydro-isostasy effects. This is the reason why around the Grande Terre, some raised beach-rocks, abraded reef flats and microatoll corals exposed up to more than 1 m above the modern sea level, dated of the mid-Holocene, can be found (mid-Holocene). These morphological features and reef structuration are dependent on the hydro-isostatic readjustment consequently to the last deglacial sea level rise from  $-120 \text{ m}$  to the modern sea level and depending on the underlying mantle viscosity (Cabioch et al., 1996). Such a process also explains the distribution and the morphological variations of the modern coral reefs and coastlines.

## History of coral reefs and lagoons

The development of the New Caledonian fringing and barrier reefs and the nature and distribution of their biofacies were documented by several studies performed on cores made mainly around the Grande Terre (Coudray, 1976; Fontes et al., 1977; Cabioch et al., 1995, 2008; Cabioch, 2003). These cores are composed of alternating layers of coral and coralline algal frameworks, detrital facies, sands, and gravels. Moreover, these cores revealed that the fringing reefs are characterized by the succession of two reef generations, while the barrier reefs by several reef or carbonate unit generations, all separated by unconformities resulting of emersion during the low sea stands. It appears that the reef growth results from the combination of both tectonic and climatic factors. The history of the lagoons is not well known, but recent bathymetric and seismic surveys documented our knowledge on the structure of the southwest lagoon.

## Fringing reefs

In the fringing reefs of the Grande Terre, coral dating in 37 cores, drilled along perpendicular or parallel transects on the reef flat, shows that the initiation growth stage is generally missing and that the reefs started to grow very quickly and suddenly (Figure 2) (Cabioch et al., 1995).

In the south, the growth started prior to 5 ka BP upon old reef karstic formations and in the north after 4.2 ka BP, generally upon non-carbonate rocks, mainly metamorphic rock (Cabioch et al., 1995; Cabioch, 2003). These differences in initiation age would be explained by unavailable suitable foundations and also as resulting from colonization of various types of substrates, the karstic limestone surfaces being probably the most suitable substrate for coral-larval and attachment recruitment. Core analysis also shows that framework, generally, dominates over skeletal debris in the higher energy reefs, while skeletal debris are the main components in the lower energy reefs (Cabioch, 2003). Moreover, the branching and tabular coral assemblages (acroporids) are mainly developed during the early stages of reef growth, whereas the domal (faviids, poritids) and/or robust-branching (acroporids) assemblages appeared later (Figure 2). Unfortunately, the reef slope and front edge zones were not investigated by coring so that two interpretations were proposed to explain this observation (Cabioch, 2003): a progressive succession from low-energy to high-energy water environments interpreted as a progressive increase of water energy as the reef approaches the sea surface, typical of a catch-up reef growth mode (Growth classification and sea level); or alternatively, a transition from lagoonal deposits typified by coral and skeletal debris to reef coralgal biofacies interpreted as a reef initiation, retrograded over its back-reef. Examination of the distribution of reef facies from reef to reef also provides additional information and shows a strong relationship with the antecedent topography (Antecedent platforms) and the local water-energy conditions. The high water energy

reefs characterized by steeply dipping antecedent platforms are dominated by frameworks while medium water energy reefs by abundant reef detritus.

## Barrier reefs

The history and the development of barrier reefs in New Caledonia are less known because it is more difficult to drill in the barrier reef tracts strongly exposed to the oceanic conditions. One of the first studies was performed by Coudray in 1976 at Ténia, on the west coast (Figure 1). Analysis of the 226 m-long core revealed the occurrence of several episodes of reef development during several interglacial quaternary stages. More recently, cores recovered at Amédée in the southwest and Kendec in the northwest (Figure 1) (Cabioch et al., 2008) showed that the New Caledonian barrier reefs are composed of a succession of depositional units resulting from a combination of glacio-eustatic sea level variations and subsidence (Antecedent platforms). In both areas, 11 carbonate units deposited during the high sea stands are observed, separated by unconformities resulting from emersion during the glacial periods (low sea stands). It appears that the reef growth would have begun around 400 ka in marine isotope stage 11, considered as a particularly favorable period for coral development. Prior to this period, the carbonate units are not characterized by biofacies typical of coral reefs *sensu stricto* although scarce isolated corals can be found.

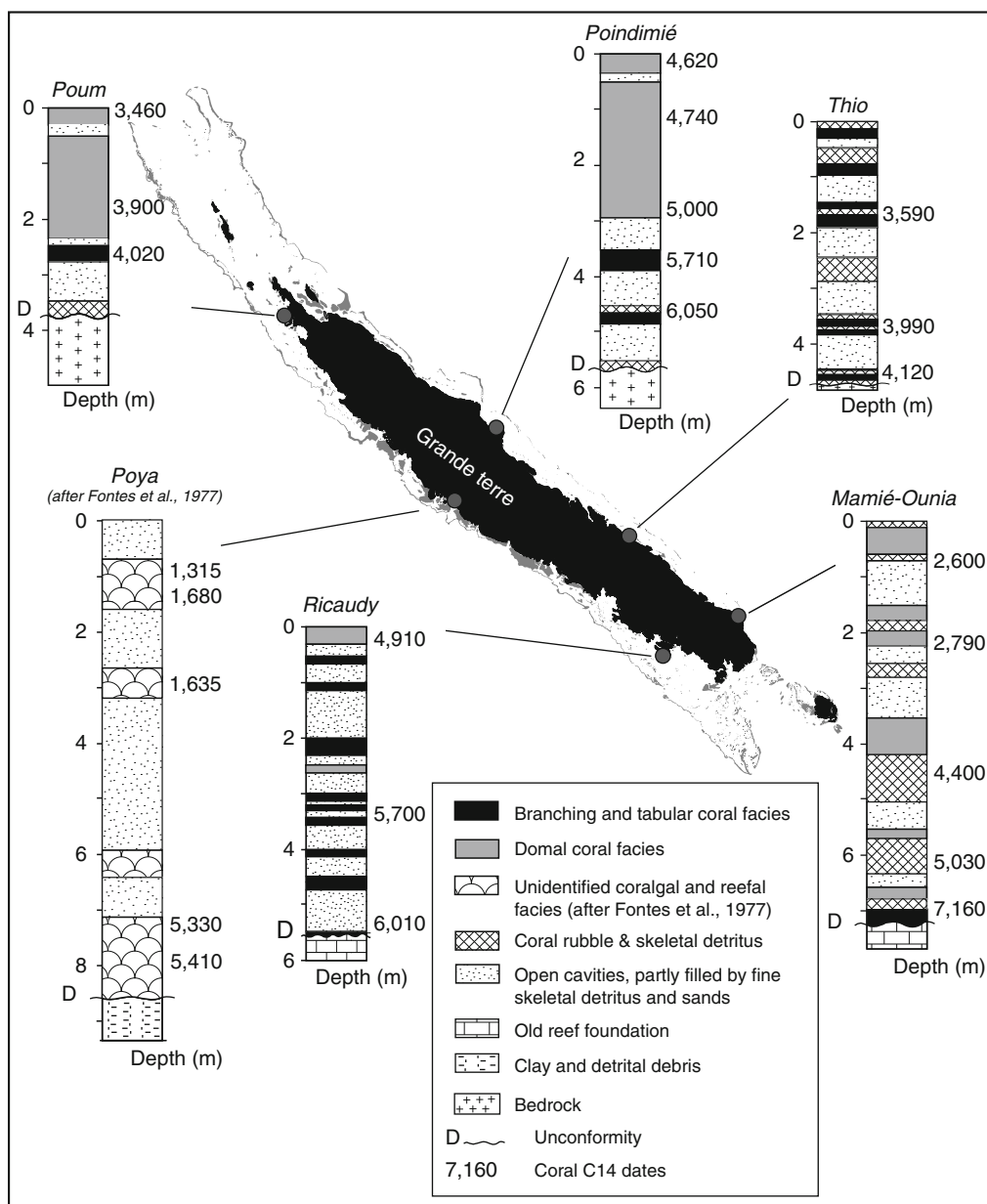
## Lagoon

Lagoons are the transition between the two morphological features of the fringing and barrier reefs, but their history is still little known. Nevertheless, a recent high resolution seismic and multibeam surveys of the South-West lagoon (Figure 1) has revealed several depositional sequences bounded by erosional unconformities, indicating two periods of deposition and erosion in the past 200 ka (Leroy et al., 2008). Two generations of incised deep fluvial valleys, connected by passes to the continental slope, were identified. These data would indicate that the lagoonal history does not extend beyond 200 ka. In addition, the analysis of morphology of this network of drainage suggests a progressive south-westward tilt of the outer lagoon expressing the role of tectonics in the formation of the lagoons.

## Climatic and/or oceanographic factors affecting the reef growth and the coral development

The distribution and the growth of modern fringing and barrier reefs are dependent not only on the tectonic context but also on the climatic variations. The climatic variations at the scale of the last 100,000 years (astronomical theory), marked by sea-level variations of the glacial and interglacial periods, influenced the internal structure and reef succession in the barrier reef tracts (see above the history of Barrier reefs). At the scale of the Holocene, the oceanographic factors and climatic variations influenced on the initiation and growth of both barrier and fringing reefs.





**New Caledonia, Figure 2** Typical biofacies from selected cores performed in the fringing reefs of the Grande Terre (modified after Cabioch et al., 1995; Cabioch, 2003).

Montaggioni et al. (2006) concluded that the upwellings seem to have been more active than today at about 6 ka, marked by occasional brief cooling events, while the SST was 1°C higher than now, explaining that the retardation of the reef development in the southwest areas of New Caledonia. It appears that nutrient supply from upwelling may have a major role in the control of the reef growth.

### Summary

New Caledonia is characterized by a broad diversity of continental and oceanic reef structures, but at this day,

only the growth history of fringing and barrier reefs from the main island or Grande Terre was intensively investigated and relatively well known. It appears that the morphology and the distribution of modern reefs can be explained by several parameters: (1) the nature and the morphology of the antecedent topography resulting of both vertical motions and climatic factors; (2) the growth pattern depending on variations of local ecological factors and oceanographic factors including SST and SSS data and also the nutrient supply from upwellings. Moreover, this region appears to be a key region to analyze the reef

episodes of the various interglacial periods. Studies from two sites in New Caledonia showed that the coral reefs probably flourished only since 400 ka.

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## Cross-references

[Antecedent Platforms](#)  
[Barrier Reef \(Ribbon Reef\)](#)  
[El Niño, La Niña, and ENSO](#)  
[Emerged Reefs](#)  
[Forereef/Reef Front](#)  
[Fringing Reefs](#)  
[Glacial Control Hypothesis](#)  
[Holocene Reefs: Thickness and Characteristics](#)  
[Last Glacial Interstadials](#)  
[Last Interglacial and Reef Development](#)  
[Mid Holocene](#)  
[Pacific Coral Reefs: An Introduction](#)  
[Paleoclimate from Corals](#)  
[Sea Level Change and Its Effect on Reef Growth](#)

## NOTCH AND VISOR

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## Definition

A notch is a horizontal intertidal recess in a solid coastline. The upper rock protruding over the recess below gives rise to the allusion to a “visor” as it can appear to be like a raised opened visor on the helmet of a suit of armor ([Figure 1](#)).



**Notch and Visor, Figure 1** Notch and visor from Aldabra Atoll, Indian Ocean (Photo: S.T. Trudgill).

Two conditions are necessary for the formation of a notch (1) a focus of erosive agencies in the intertidal and (2) relatively sheltered conditions because on high-energy coasts wave action would tend to act to remove the upper projecting rock. The erosive agencies may involve abrasion by sand, especially in the lower part of the notch but generally involve bioerosion by boring organisms, such as sponges and bivalve molluscs, which bore into the rock to avoid desiccation and organisms which graze on epi- and endolithic algae such as chitons and gastropod molluscs. These are focused in the intertidal zone as it is too dry for them to survive above and they tend to be outcompeted by other organisms below, hence giving greater erosion in the intertidal zone and the notch.

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### Cross-references

[Algae, Blue-Green Boring](#)  
[Bioerosion](#)  
[Molluscs](#)  
[Solution Processes/Reef Erosion](#)  
[Sponges](#)

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## NUTRIENT POLLUTION/EUTROPHICATION

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### Synonyms

Eutrophication; Nutrient pollution; Organic enrichment

### Definition

Eutrophication defines the process of increasing the rate of supply of plant nutrients (especially nitrogen and phosphorus) and organic matter to an ecosystem. A contaminant is defined as a substance (including nutrients and sediments) that occurs above “natural” concentrations, while the term “pollutant” defines a contaminant that occurs at a concentration that causes environmental harm (e.g., changes in physical, chemical, or biological properties; biogeochemical functions; and/or biological community structures of a system).

### Summary

Nutrient pollution or eutrophication has severely degraded many coastal reefs around the world. The three main pathways of reef damage by nutrient pollution are release of nutrient limitation (nitrogen, phosphorus, or organic matter), light limitation from increased turbidity, and flow-on effects from altered sediment properties. While nutrients, light, and sediments also vary greatly in areas unaffected by humans, they are often elevated from land clearing, agricultural and urban runoff, and aquaculture. Eutrophication leads to reduced recruitment and species richness in reefs and altered trophic structures (corals being replaced by macroalgae in shallow water and by heterotrophic communities in deeper water). On Indo-Pacific reefs, nutrient pollution may also lead to increased frequencies of outbreaks of the coral-eating starfish, *Acanthaster planci*. The vulnerability of a specific reef area to damage by eutrophication is greatest if it is located in a poorly flushed location or surrounded by a shallow sea floor. Reefs that are frequently disturbed and reefs with low abundances of herbivorous fishes are also sensitive to degradation by nutrient pollution. In contrast, reef areas that are flushed by fast currents or surrounded by a deep



water body and reef areas with abundant herbivores are relatively resistant to exposure to nutrient pollution.

### What is eutrophication?

Eutrophication, or nutrient pollution, is defined as the process of enrichment of waters with plant nutrients and organic matter, often resulting in a chain of trophic changes. Eutrophication is typically caused by the elevated supply and availability of the macronutrients nitrogen (N) and/or phosphorus (P), which stimulate the growth of microbes, micro- and macroalgae, and lead to an increased supply of organic matter. This in turn alters the physical and chemical environment by reducing water clarity and organically enriching sediments and eventually results in potentially profound changes in biogeochemical, physiological, and ecological conditions. If the nutrients and sediments leading to eutrophication occur at a concentration causing such environmental harm, they fit the definition of “pollutants.” Minor cases of eutrophication, i.e., if they occur at above “natural” concentrations without causing environmental harm, they fit the definition of “contaminants.” Nutrient pollution is only one of the many forms of aquatic pollution, others being pollution by pesticides, industrial effluents, pharmaceuticals, oils spills, fecal bacteria, etc., which are not being covered here. Nutrient levels can also be quite high in some undisturbed ecosystems, yet when human activity elevates nutrients in environments with naturally low nutrient availability, the resulting conditions may be far removed from natural equilibria. The relative trophic state of aquatic ecosystems is sometimes classified as “oligotrophic” (low nutrient availability), “mesotrophic,” or “eutrophic” (relatively high nutrient availability, either naturally or from nutrient pollution). This classification is only of limited use and should only be applied when comparing within ecosystems’ types, because a eutrophic lake typically has far higher nutrient concentrations than a eutrophic coastal marine water body. However, it is important to understand that all of these ecosystems may be subject to eutrophication, i.e., an anthropogenic enrichment with nutrients compared to their previous state. Due to its cascading effects on ecosystems and the incremental changes from natural overcontaminated to polluted conditions, the question of nutrient pollution is very complex and broad in scope.

Well-described symptoms of eutrophication are increased phytoplankton production, bacterial and fungal growth, an increased frequency of visible algal blooms (such as red tides) or marine snow aggregates, and/or the massive development of attached and/or floating algal mats (Vollenweider, 1992). Further, water transparency is often reduced from suspended detritus, mineral particles, and plankton, and dissolved oxygen levels in the bottom waters may be depleted and can cause fish kills. Economic consequences attributed to severe eutrophication include a reduction in the health of shellfish, fish, and benthos; reduced tourism; ciguatera shellfish

poisoning; and potential effects on human health from dermatitis or conjunctivitis (Vollenweider, 1992). However, the symptoms of eutrophication are not always consistent and predictable across the World’s aquatic ecosystems.

Eutrophication is usually caused by the excessive runoff of fertilizers from farms, soil-bound nutrients from cleared lands, sewage effluents, or discharges from aquaculture into a poorly mixed or partly enclosed water body. The amount of nutrients and sediments lost from a catchment is well predicted by its geographic features including soil type, slope angle, and rainfall. Additionally, soils and fertilizers flow from cleared and overgrazed lands, sewage, or aquaculture farms into coastal marine ecosystems, including coastal coral reefs (Vitousek et al., 1997; Tilman et al., 2001; Smith et al., 2003). Globally, the use of nitrogen fertilizer has increased more than 6-fold since 1960 (Matson et al., 1997), and an additional 1% of the earth’s surface is being cleared every year. About 45% of the global human population ( $\sim 100$  people  $\text{km}^{-2}$ ) are now living in coastal areas, and human population is growing even faster along the coast than elsewhere: the number of people living in the coastal area has increased by 765 million to  $\sim 3.1$  billion people since 1990 alone (Crossland et al., 2005). All this contributes to increasing losses of nutrients from the land and a rapidly intensifying exploitation of coastal resources (Crossland et al., 2005). Oxygen-depleted seafloor zones, attributable to runoff of agricultural nitrogen and phosphorus, have doubled in area in the last few decades – indicating that many marine water bodies are becoming more eutrophic (Diaz and Rosenberg, 2008; Vaquer-Sunye and Duarte, 2008).

### Effects of nutrient pollution and eutrophication on coral reefs

Coral reefs can be found in nutrient, light, and sedimentation conditions that may vary, both spatially and temporally, by 1–2 orders of magnitude even in undisturbed settings. New dissolved and particulate inorganic and organic nutrients and sediments may originate from rivers, the upwelling of nutrient-rich deeper water bodies, nitrogen fixation by benthic and pelagic cyanobacteria and algae, diffuse coastal runoff, groundwater seepage, and rain and settling dust from the atmosphere. Reef communities naturally change with nutrient, light, and sedimentation conditions: from terrestrially influenced conditions (characterized by fluctuating salinity, more variable or higher nutrient load, siltation, and turbidity) to oceanic conditions where nutrients, siltation, and turbidity are typically low. Reef environments are not typically classified by their trophic state (i.e., oligo-, meso- or eutrophic), but reefs in all trophic states may be affected by eutrophication.

Coral reefs are built by the calcium carbonate skeletons of hard corals (order Scleractinia), which live in symbiosis with endosymbiotic unicellular algae (zooxanthellae). The tens of thousands of species associated with coral reefs

depend on the structural complexity derived from coral skeletons, and the ecological condition of coral reefs is, therefore, a direct function of the physiological health of hard corals. Hard corals are highly competitive in low-nutrient environments, for three reasons. First, they are remarkably efficient in internally recycling nutrients between host and zooxanthellae. Second, they occupy most trophic levels simultaneously (Houlbreque and Ferrier-Pages, 2009): the photosynthesis of the zooxanthellae makes them efficient phototrophs; they can absorb dissolved nutrients, graze on large phytoplankton, prey upon zooplankton, and feed on detritus and other decompositional material (Rosenfeld et al., 1999). Third, some species of hard coral can rapidly adapt to varying light and food availability, maximizing energy gains throughout their lifetime (Anthony and Fabricius, 2000). Despite the high adaptability of corals to a range of environmental conditions, reports of coral reef degradation from eutrophication exist from many places around the world (reviewed in Fabricius, 2005). However, the natural variability in background conditions and the paucity of historical data make it often difficult to ascertain causal relationships between eutrophication and reef degradation. Furthermore, other disturbances (e.g., overfishing, coral bleaching, storms, and floods) complicate the assessments. Epidemiological tools originally developed to assess the weight of evidence that smoking causes lung cancer (U.S. Department of Health, 1964) have now been applied to coral reef studies to create a causal link between reef degradation and increased exposure to nutrient pollution in the central Great Barrier Reef (Fabricius and De'ath, 2004).

Eutrophication degrades coral reefs through three pathways (a) trophic changes from the increased availability of nutrients and organic matter; (b) decreasing light availability in deeper water; and (c) altered sediment properties. The following sections briefly review the available information on how these three pathways, alone and in combination, directly and indirectly affect corals, other reef-associated organisms, and the ecological balances of coral reef ecosystems.

### Effects of the increased availability of nutrients and organic matter

Eutrophication increases the availability of nutrients and organic matter both in the water and in the sediments. Dissolved and particulate and organic and inorganic nutrients are often treated separately, as their biological effects differ fundamentally. For example, dissolved inorganic nutrients such as phosphate, nitrate, and ammonium are highly bioavailable and therefore get quickly depleted, whereas many forms of dissolved organic nutrients are largely unusable as food even for bacteria and therefore often accumulate to high concentrations. However, cycling between the different forms of nutrients is fast and complex, due to uptake, excretion, and decomposition in benthic and pelagic food webs that ensure continuous

conversions between dissolved and particulate and between organic and inorganic forms of nutrients.

Studies of eutrophication effects on corals have often focused on enrichment with dissolved inorganic nutrients (e.g., Stambler et al., 1994; Dubinsky and Stambler, 1996; Koop et al., 2001; Szmant, 2002). Exposure to dissolved inorganic nitrogen may lead to declining calcification, higher concentrations of photopigments (affecting the energy and nutrient transfer between zooxanthellae and host; Marubini and Davies, 1996), and higher rates of coral diseases (Bruno et al., 2003). In areas of nutrient upwelling or in heavily polluted locations, chronically increased levels of dissolved inorganic nutrients may alter coral physiology and calcification, causing noticeable changes in coral communities (Birkeland, 1997). However, although high levels of dissolved inorganic nitrogen and phosphorus can cause significant physiological changes in corals, they do not kill or greatly harm individual coral colonies (reviewed in Fabricius, 2005). Furthermore, biological uptake by bacteria, phytoplankton, and the benthos rapidly convert dissolved inorganic nutrients into particulate organic matter (especially detritus, bacteria, phytoplankton, and marine snow), hence their concentrations in the water column are often low even in areas of eutrophication.

The main pathway how dissolved inorganic nutrients affect coral reefs is by organic enrichment of suspended particulate matter and sediments. Pelagic particulate organic matter is often measured using chlorophyll, total suspended solids, and/or particulate nitrogen and phosphorus as proxies. Particulate organic matter may alter benthic irradiance, may organically enrich sediments, and may lead to hypoxia in sediments. These secondary effects are, additionally to nutrient enrichment, significant eutrophication effects. Particulate organic matter is used by corals as food, and their tissue thickness, photosynthetic pigment concentrations, and calcification increase in response to feeding on particulate organic matter. At moderate levels of eutrophication, some hard coral species can compensate for lost photosynthetic carbon gains by increasing particle feeding, while other species become saturated at low particle concentrations and are unable to compensate for light loss (Anthony and Fabricius, 2000). At even higher levels of eutrophication, gross photosynthesis and respiration, tissue thickness, and calcification start to decline in all species as light attenuation outweighs further energy gains from particle feeding. Photosynthesis, tissue thickness, and calcification therefore change in a modal fashion along eutrophication gradients (Tomascik and Sander, 1985; Marubini and Davies, 1996). In contrast, photosynthetic pigment concentrations in corals further increase with increasing eutrophication, and have, therefore, been suggested as a useful measure for eutrophication (Marubini, 1996; Cooper et al., 2009).

While corals are not directly harmed by dissolved inorganic nutrients and, within bounds, benefit from particulate organic matter, both macroalgae and heterotrophic filter feeders greatly benefit from dissolved inorganic

and particulate organic nutrients, more than corals do. Macroalgae use photosynthesis to obtain carbon and meet their nutrient demand through uptake of dissolved inorganic nutrients, plus, in some species, through demineralization of particulate organic matter deposited on their fronds (Schaffelke, 1999). In the absence of control by herbivores, some groups of macroalgae are nutrient limited and increase in growth and biomass at minute increases in dissolved inorganic nutrients and particulate organic matter (Littler and Littler, 2007). Similar to the widely observed symptoms of eutrophication in other aquatic ecosystem, macroalgae dominate coral reefs with high nutrient availability, including in areas of eutrophication (Smith et al., 1981; Lapointe et al., 2004; Lapointe and Bedford, 2007). Long-term data have shown that expanding (Cuet et al., 1988) or declining (Smith et al., 1981) macroalgal cover coincides with increasing and declining nutrient availability, respectively. These time series data indicate a causal link between macroalgal abundances and nutrient availability. On the Great Barrier Reef, total macroalgal cover increases 5-fold from highest to lowest water clarity and additionally 1.4-fold from lowest to highest chlorophyll, 3.3-fold from offshore to inshore, and 3.1-fold from northern to southern reefs (De'ath and Fabricius, 2010). Macroalgae also tend to flourish in areas of nutrient upwelling, on eastern sides of continents or large islands where more rivers originate than in the west (Birkeland, 1988), and towards higher latitudes, as do nutrient concentrations (Johannes et al., 1983). These large-scale geographic data all add evidence that nutrient levels influence macroalgal biomass. However, increases in macroalgal biomass are only observed in areas where grazing by herbivorous fishes or invertebrates is too low to control abundances (McCook, 1999; Littler and Littler, 2007) and where light levels are sufficient.

All dense macroalgal assemblages, be it low and often ephemeral mats, or taller and often perennial stands, suppress coral recruitment through space occupancy, allelopathy, silt-trapping, or shading (Connell et al., 1997; Szmant, 2002). Mat-forming macroalgae tend to also damage or kill understorey corals by restricting gas exchange and creating hypoxia when mats collapse (Loya et al., 2004). Tall perennial macroalgae, such as *Sargassum* spp., do not usually kill corals, but they can reduce coral growth by shading and tissue abrasion (Littler and Littler, 2007). As a result, corals may be outcompeted by macroalgae that grow best in high-nutrient environments – as long as light is not limiting.

Another severe consequence of eutrophication is the increased probability of outbreaks of the coral eating crown-of-thorns starfish *Acanthaster planci* (Birkeland, 1982; Brodie et al., 2005). *A. planci* has been the most prominent cause of coral mortality throughout many tropical Indo-Pacific regions in the last four decades. The pelagic planktotrophic larvae of this starfish filter-feed on large phytoplankton, and experiments suggest that these larvae are food limited: their survivorship in the

laboratory increases steeply with increasing availability of suitable food at environmentally relevant concentrations (Fabricius et al., 2010). In the field, increased nutrient availability can increase the abundance of large phytoplankton cells: a strong temporal and spatial relationship exists between drought-breaking floods from high continental islands and outbreaks of this starfish (Birkeland, 1982). New research further strengthens the evidence that more frequent outbreaks of *A. planci* are linked to high nutrient levels (Brodie et al., 2005; Houk et al., 2007). After primary *A. planci* outbreaks have formed in a region with high phytoplankton concentrations, many of their numerous larvae may be transported by currents to remote regions, hence secondary *A. planci* outbreaks may form far away from areas of eutrophication.

Benthic filter feeders, including sponges, bryozoans, bivalves, barnacles, and ascidians, are important components of reef ecosystems. Most filter feeders feed on the smallest fraction of plankton and few obtain a positive carbon balance in oligotrophic waters (Birkeland, 1988). Most benthic filter feeders live in crevices or bore holes into coral skeletons to avoid predation, and as cryptofauna they are not associated with photosynthetic endosymbionts. Fewer live on the reef surface, and these often contain photosynthetic endosymbionts, possibly accelerating growth thus enabling them to compete with hard corals and algae for space. Filter-feeder densities increase in response to nutrient enrichment, but surface-inhabiting filter feeders rarely outcompete corals for space even in eutrophic environments (Aerts and Van Soest, 1997). The few observed cases of space monopolization by a filter feeder were restricted to areas of low light, high plankton productivity, and organic enrichment (Smith et al., 1981; Brock and Smith, 1983), i.e., conditions that are unsuitable for corals. The demise of corals and the establishment of filter feeders are therefore largely independent symptoms of eutrophication, with the fate of each group determined by altered trophic conditions rather than by altered balances in space competition.

Many cryptic filter feeders are macro-bioeroders that actively bore into or chemically erode the calcium carbonate skeletons of live corals and dead reef substrata. They include boring sponges (e.g., *Cliona* spp.), bivalves (e.g., *Lithophaga* spp.), sipunculans, and polychaetes (Hutchings, 1986). Several studies have documented abundances of internal macro-bioeroders increasing in response to increased nutrient availability (Rose and Risk, 1985; Hallock, 1988; Cuet et al., 1988), and abundances of most internal macro-bioeroders are higher in productive inshore environments than they are offshore. Increased bioerosion in areas of nutrient enrichment can substantially weaken the structure of coral framework and increase storm damage. This, combined with reduced coral growth, diminished skeletal densities, and lower recruitment rates, can mean that reef erosion exceeds calcium carbonate accretion due to eutrophication (Pari et al., 2002).



### Effects of decreasing light availability due to turbidity

Benthic irradiance is an important factor determining the ability of organisms to conduct photosynthesis. At a given water depth, it is strongly governed by sediment resuspension, phytoplankton productivity, and other forms of particulate and dissolved organic matter. Sediments with large grain sizes settle near the source (e.g., in river deltas), but the smallest sediment fractions (clay and silt particles) remain suspended for days to weeks, during which times they may be transported over tens to hundreds of kilometers. Compared with larger grain sizes, these small particles absorb more light (Moody et al., 1987) and carry more nutrients and pesticides (Gibbs et al., 1971). Historic data on water clarity in marine systems are, however, sparse, and the conditions leading to long-term changes in water clarity in tropical coastal systems are poorly understood. Exceptions are records of reduced water clarity around a sewage outfall site in Kanehoe Bay, Hawaii (Hunter and Evans, 1995), and around floating fish farms in the Northern Red Sea (Loya et al., 2004).

Benthic irradiance is an essential environmental factor for corals, seagrasses, and algae. Corals can acclimatize to changing irradiance by altering their pigment density. As photoacclimation takes about 5–10 days, it is too slow to compensate for energy losses at fluctuating turbidity (Anthony and Hoegh-Guldberg, 2003). Shading from turbidity, therefore, leads to slower coral calcification and thinner tissues. Coastal coral reefs in turbid water, therefore, tend to be restricted to the upper 4–10 m compared to >40-m depths in clear oceanic waters (Yentsch et al., 2002). Reef development tends to cease at around 4–8% mean surface irradiance (Yentsch et al., 2002; Cooper et al., 2007). Coral cover and species richness decline with increasing depth at high turbidity, with the most phototrophic species being the first to disappear. Importantly, macroalgae are also missing at deeper depths despite the high availability of nutrients, as they are quickly light limited (Hillebrand, 2005). On these dark reef slopes, filter-feeder communities may be prolific. In turbid but shallow water, both light and nutrient levels are high and coral cover and coral growth rates may be very high – but only if herbivores are effective in keeping macroalgae in bay and if hydrodynamics prevent the accumulation of sediments. If herbivores are missing, the slow-growing corals tend to be outcompeted by fast-growing macroalgae.

Fishes play an essential role in the ecology of coral reefs, with low abundances of herbivorous fish potentially leading to a proliferation of macroalgae and declining coral cover (Hawkins and Roberts, 2004). Importantly, the abundance of herbivorous fish on coral reefs may potentially decline not only from overfishing, but also from nutrient pollution. Wolanski et al. (2004) reported a negative relationship between water clarity and the abundance of herbivores on the Great Barrier Reef, and a similar result was found along a water-quality gradient

in the Caribbean (Mallela et al., 2007). On the Great Barrier Reef, herbivorous fish are not usually targeted by fishers suggesting minimal fishing pressure, yet macroalgae cover extensive areas on many inshore reefs (De'ath and Fabricius, 2010), suggesting that control by herbivores is ineffective. The mechanisms for the apparent negative relationship between abundances of herbivorous fishes and poor water quality is still poorly understood; they may include an avoidance of turbidity (Wolanski et al., 2004) or a reduced food palatability, if algae trap large amounts of sediments (Mallela et al., 2007). If such negative relationship was more widespread than presently realized, then water quality would not only directly but also indirectly promote macroalgae, by releasing both nutrient limitation and grazing pressure. A systematic investigation of the potential relationships between water quality and the abundance herbivorous fishes is urgently needed.

### Effects of altered sediment properties

Coastal nutrient pollution is often linked to altered sediment properties or sedimentation regimes. Coarse sediment grains usually settle within a few kilometers of the discharge source, often contributing to forming river deltas. However, fine particles including detritus, clay, and silt particles may remain suspended for prolonged periods of time. These fine particles carry a large proportion of the total river load of nutrients and pesticides, which eventually settle onto the seafloor and onto the benthic organisms, sometimes tens to hundreds of kilometers away from the source.

Previous studies have mostly focused on assessing the effects of increased rates of sedimentation on coral reefs. Sedimentation rate is a strong environmental driver for coral reefs. It is known to reduce coral recruitment rates and coral biodiversity, and many sensitive species are missing or underrepresented in areas of high sedimentation (Rogers, 1990; Fabricius, 2005). Photophysiological stress in corals increases linearly as the product of the duration and amount of sediment exposure, i.e., two units of sediment deposited on the coral for one time unit, exerts a similar decline in photosynthetic yields as half the amount deposited for twice the time (Philipp and Fabricius, 2003). High sedimentation rates (up to 100 mg dry weight  $\text{cm}^{-2}$ ) can kill exposed coral tissue within a few days. Exposure to a few days of sedimentation can therefore cause long-term damage to coral populations, by removing whole cohorts of small and sensitive corals. Previous studies have suggested a sedimentation threshold of 10 mg  $\text{cm}^{-2} \text{ day}^{-1}$ , as reefs may be severely damaged at higher rates (Rogers, 1990).

Eutrophication may, however, not always increase the rate of sedimentation, but may alter sediment properties. Experiments have shown that when coral tissue is exposed to sedimentation, the degree of damage increases with bacterial activity (Hodgson, 1990) and with decreasing grain sediment sizes (Weber et al., 2006). Nutrient-rich sediments and sediments with high organic contents cause

greater stress and damage to corals than do sediments that are poor in organic matter (Weber et al., 2006). Fine and organically enriched sediments may support different bacterial communities and metabolic processes, further altering the microenvironment on the reefs biofilm surfaces. Fine sediments may also bind with marine snow aggregates, and this additional organic material is highly damaging to coral recruits (Fabricius et al., 2003). At very high levels of pollution, the decomposition of organically enriched sediments can lead to hypoxia in poorly flushed and highly stratified locations, further damaging benthos. Not only the amount of sedimentation and its geochemical and physical properties, but also its biological properties and organic contents are ecologically relevant and determine the extent of sedimentation damage in coral reefs.

Corals are most sensitive to sedimentation during their recruitment stage, and reduced coral recruitment is one of the most deleterious effects of eutrophication on coral reefs. Coral settlement is sparse on sediment-covered surfaces, and the tolerance of coral recruits to sediment is at least one order of magnitude lower than that of adult corals (Fabricius, 2005). Newly settled corals may be killed by exposure to  $12 \text{ mg cm}^{-2} \text{ day}^{-1}$  for  $<48 \text{ h}$  if the sediment is bound by marine snow and rich in organic contents, but can tolerate such levels if the sediments are low in organic content (Fabricius et al., 2003). These and similar data demonstrate the critical role of organic sediment enrichment and the interactions of nutrients and sediments on the effects on coral reefs.

Certain species of crustose coralline red algae are essential for coral settlement. While high nutrient levels do not greatly alter the physiology of crustose coralline algae, high sedimentation rates are related to low coralline algal cover in coral reefs (Kendrick, 1991; Fabricius and De'ath, 2001). Some coralline red algae survive burial under coarse inorganic sediments for days to weeks, but their survival rates rapidly decline if the sediments contain traces of herbicides (Harrington et al., 2005). Turf algae often outcompete coralline algae, and by trapping sediments they can make the substratum unsuitable for coralline algae and for coral settlement (Birrell et al., 2005).

### Factors determining the vulnerability of a specific coral reef to eutrophication

Effective coastal management requires an understanding of the factors that determine the vulnerability of specific coral reefs to eutrophication. Vulnerability may vary depending on the reef's exposure, resistance, and resilience.

The degree of exposure of an organism or ecosystem to a stressor is typically a function of the amount (= concentration, level, or load) of the stressor and the length of time it is in contact with the stressor. A reef may be exposed to a high level of a stressor for a short period of time or to lower levels for longer periods. When quantifying exposure levels, it is important to determine peak concentrations (potentially leading to damage or mortality within

hours to days), as well as to quantify long-term mean (or median) concentrations and the duration of exposure.

The resistance of an ecosystem is defined as the ease or difficulty with which it changes when exposed to a disturbance (Pimm, 1984). Resistance can arise from prior exposure history, environmental factors, or biological factors (Done, 1999; West and Salm, 2003). For example, a coral reef that has developed in a naturally turbid setting and is dominated by corals of the turbidity-tolerant genera *Turbinaria* and massive *Porites* is more resistant to change from exposure to nutrient pollution than an *Acropora*-dominated reef that has developed in clear waters. Ecological resilience is defined here as the time it takes for an ecosystem to return to its equilibrium point after being disturbed (Nyström et al., 2008).

A review of some of the better-described case studies in the literature allows to qualitatively identify the main factors that predict the exposure, resistance, and resilience of specific reefs to degradation. Currents are extremely important properties of coral reefs and are key predictors of exposure, resistance, and resilience at both local and regional scales. At local scales, current-swept reef fronts, flanks and channels, and reef crests with moderate wave exposure are the least likely to retain pollutants; they support high recruitment and have the fastest coral growth (Sebens, 1991). Ideally, wave exposure is sufficient to remove sediment deposits without causing frequent coral breakage. As fast currents and waves also facilitate macroalgal growth, competition between corals and macroalgae is intense if nutrient levels are high. At regional scales, currents determine where and how far pollutants are being transported. Where currents are predominantly tidal, a very low or very high tidal range diminishes the ability of reefs to withstand pollution, by affecting circulation. Currents that create a strong connectivity to source populations of pelagic larvae also improve the resilience of a reef, by decreasing the time of recovery from a disturbance.

The exposure of a coral reef is furthermore well predicted simply based on spatial factors: the closer downstream a coral reef is to a pollution source and the higher the mean annual load of this source, the greater is its exposure to a pollutant (Bryant et al., 1998). Geospatial models of the global scale of pollution around coral reefs have been developed based on the distance of reefs to pollution sources (Bryant et al., 1998). These models estimate that 22% of all coral reefs worldwide are classified as at high or medium threat from inland pollution and soil erosion. The global models also classify 12% of reefs at threat from marine pollution (distance from ports, oil tanks, oil wells, and shipping areas) and 30% of reefs as threatened from coastal development such as cities, mines, and resorts (Bryant et al., 1998). At regional scales, the percentage of reefs at risk is a direct function of the extent of land clearing, and up to 50% of reefs is at risk in the countries with the most widespread land clearing (Bryant et al., 1998). At local scales, such as downstream from well-defined point sources

or in coastal reefs fringing eroding land, terrestrial runoff can be the single most significant pressure for selected coral reefs (Bourke et al., 2002). However, such geospatial models do not factor in additional indirect effects that may occur hundreds of kilometers away from areas of eutrophication, such as increasing frequencies of outbreaks of coral eating crown-of-thorns starfish populations.

Topography/geomorphology and bathymetry can modify exposure enormously: pollutants are retained for prolonged periods in poorly flushed embayments and lagoons with reduced circulation or small water volumes, whereas they may be rapidly washed away from a headland surrounded by a deep water body (Hopley et al., 2007). Around the world, most severely polluted and hypoxic marine sites are located in shallow and poorly flushed semienclosed waterbodies such as gulfs, bays, fjords, or bights (e.g., Kaneohe Bay, the Baltic Sea, Chesapeake Bay, Irish Sea; Diaz, 2001). Bathymetry also modifies exposure by affecting the balance between sedimentation and resuspension of materials. Materials are easily washed away from shallow, upper reef slopes, but accumulate below the reach of surface waves in deeper areas (Wolanski et al., 2005). Upper reef slopes are also less affected by turbidity than are deeper areas, where light becomes limiting for photosynthetic organisms. Exposure is worst at sites surrounded by a wide, shallow continental shelf where materials are repeatedly wave resuspended, whereas pollutants are flushed away into deeper waters if no shelf retains them. For example, the Great Barrier Reef is located on a 50–200-km-wide shallow continental shelf with >2,000 individual coral reefs between the land and the open ocean. Retention times here are still being debated, but some estimate them to be up to 300 days for dissolved materials (Luick et al., 2007). Particulate materials are likely to be retained for even longer periods of time, as they are repeatedly deposited and resuspended from the shallow sea floor. So, although nutrient enrichment is less severe on the Great Barrier Reef than in many other more densely populated regions, symptoms such as macroalgal dominance and low coral diversity on numerous inshore reefs have been attributed to enhanced terrestrial runoff (van Woesik et al., 1999; Fabricius and De'ath, 2004; Fabricius et al., 2005; De'ath and Fabricius, 2010).

Lastly, biological processes are believed to modify the resistance and resilience of coral reefs, but many of these processes are as yet poorly understood. For example, abundant herbivorous fish strongly control macroalgal abundances, thereby promoting resilience (Littler and Littler, 2007). It is also still unresolved to what extent resistance and resilience are codetermined by biodiversity; biogeographic regions with low biodiversity have fewer species to replace the loss of sensitive species and may be more likely to undergo structural and functional changes in their communities (Bellwood et al., 2004). For example in the Caribbean, the loss of the dominant coral species *Acropora palmata* and *Acropora cervicornis* and the one remaining important algal grazer, *Diadema antillarum*, has led to a widespread collapse of reef

ecosystems (Lessios et al., 1984). It is also unknown whether or not the resistance and resilience of reefs vary along latitudinal gradients, as reefs in higher latitudes naturally have lower calcification rates, higher macroalgal biomass, and lower coral biodiversity than do low latitude reefs. Lastly, regions that are prone to severe or frequent disturbances (e.g., from coral bleaching, storms, cold water upwelling, or outbreaks of *A. planci*) are more likely to be prone to degradation than rarely disturbed regions. This is because poor water quality often does not directly kill the adult coral populations, but retards coral recruitment and hence the speed of recovery from unrelated disturbances. It has also been shown that exposure to one form of stress may decrease the resilience of an ecosystem to another stressor (Hughes et al., 2003; Wooldridge et al., 2005).

In summary, degradation from poor water quality is most likely to occur on deeper reef slopes, in locations with weak currents, in places where fish abundances are low, and in regions that are frequently affected by other forms of disturbance. In contrast, well-flushed locations with strong currents, shallow reef crests surrounded by a deep water body, and reefs inhabited by healthy populations of fishes are likely to have the highest levels of resistance and resilience.

Several of these factors are identical to those that determine the resistance and resilience of coral to bleaching caused by warming oceans. For example, topography, fast currents, proximity to deep water, and a diverse community with abundant herbivores are considered reliable factors in predicting the likelihood of coral communities dying as a result of bleaching (West and Salm, 2003) – as they are in predicting death arising from eutrophication. One difference is that reefs in shallow waters are – relative to deeper reef slopes – tolerant of the turbidity associated with eutrophication but sensitive to bleaching. A better understanding of the additive or interactive effects between eutrophication and climate change is clearly needed.

## Conclusions

Although disturbances are a normal and important aspect of their environment, coral reefs are inherently quite stable over time, with coral cover and composition often not changing for many years to decades (Connell, 1997). After severe acute and short-term disturbances, coral in shallow, well-lit windward reefs with fast currents can recover within 10–15 years, if larvae are plentiful (Connell, 1997). Recovery takes longer – possibly up to 50 years – on deeper reef slopes and in poorly flushed settings such as lagoons and areas with weak water flow and poor connectivity. Recovery from chronic and human-induced disturbances that alter the physical environment is also slower and less commonly observed than recovery from fast and acute disturbances (Connell et al., 1997). If widespread reef degradation is to be avoided, it is essential that the average frequency of severe disturbances does not



exceed the average recovery time in any one location and that chronic disturbances are minimized. In recent times, the frequency and nature of major disturbances, such as coral bleaching, outbreaks of *A. planci*, and severe storms, have exceeded the capacity of many reefs around the world to recover (Wilkinson, 2004). Such large-scale events are typically not controllable by management action. In contrast, eutrophication is much more manageable and can often be prevented by preservation of vegetation cover on land, reduction of fertilizer loss into the sea, and restriction of aquaculture facilities to well-flushed locations where dilution is rapid and the resistance and resilience of the marine ecosystems are greatest. With increasing reef disturbances as a result of global warming and seawater acidification, management of water quality and healthy fish abundances will be critically important to the future of coral reef ecosystems.

## Acknowledgments

This study was funded by the Australian Institute of Marine Science, and the Marine and Tropical Sciences Research Facility, a part of the Australian Government's Commonwealth Environment Research Facilities Program.

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## Cross-references

[Adaptation](#)  
[Algae, Coralline](#)  
[Algae-Macro](#)  
[Algae,Turf](#)  
[Bioerosion](#)  
[Bioturbation](#)  
[Climate Change and Coral Reefs](#)  
[Conservation and Marine Protection Areas](#)  
[Corals: Biology, Skeletal Deposition, and Reef-Building](#)  
[Corals: Environmental Controls on Growth](#)  
[Darwin, Charles \(1809–1882\)](#)  
[El Niño, La Niña, and ENSO](#)  
[FORAM Index](#)  
[Lagoon Circulation](#)  
[Microbes](#)  
[Ocean Acidification, Effects on Calcification](#)  
[Octocorallia](#)  
[Reef Classification by Fairbridge \(1950\)](#)  
[Reef Classification by Hopley \(1982\)](#)  
[Reef Classification by Maxwell \(1968\)](#)  
[Reef Restoration](#)  
[Sediments, Properties](#)  
[Scleractinia, Evolution and Taxonomy](#)  
[Sediment Durability](#)  
[Symbiosis; Zooxanthellae](#)  
[Temperature Change: Bleaching](#)  
[West Indian Coral Reef Classification](#)



# O

## OCEAN ACIDIFICATION, EFFECTS ON CALCIFICATION

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### Synonyms

Lowered pH of seawater

### Definition

*Aragonite*: A calcium carbonate ( $\text{CaCO}_3$ ) mineral with an orthorhombic crystal lattice structure; a polymorph of calcite.

*Calcification*: The process by which an organism secretes calcium carbonate.

*Calcite*. A calcium carbonate ( $\text{CaCO}_3$ ) mineral with a trigonal (rhombohedral) crystal lattice structure; a polymorph of aragonite.

*High-Mg calcite*: Calcite containing at least 4 mol%  $\text{MgCO}_3$ .

*Ocean acidification*: The decrease in the pH of the Earth's oceans caused by the uptake of carbon dioxide from the atmosphere.

*Rhodoliths*: Coralline algae that grow in rounded, free-living forms that are unattached to the substrate.

*Saturation state*: A measure of the thermodynamic potential of a mineral to precipitate or dissolve.

### Introduction

Technically, the term “ocean acidification” refers to any process that causes a decrease in seawater pH. Today, however, the term refers almost exclusively to the process by which oceanic water absorbs carbon dioxide from the atmosphere, causing a decrease in ocean pH and changes

in other chemical properties of seawater. Ocean acidification is not a consequence of climate change, but the two share a common cause: increasing concentration of carbon dioxide in the atmosphere. Ocean acidification can affect coral reefs in multiple ways: effects on biogeochemical processes, physiology of organisms, and even such things as sound transmission, have been demonstrated. However the best-documented effects are those on organisms that secrete calcium carbonate, most notably corals, coralline algae, and foraminifera, which are major contributors to reef growth.

### Chemistry of ocean acidification

The chemical reactions involved in ocean acidification are well documented, albeit somewhat complicated. Carbon dioxide reacts with seawater to form carbonic acid:



Most of the carbonic acid dissociates quickly to hydrogen ions (a contributor to acidity) and bicarbonate ions:



and some of the bicarbonate also dissociate to hydrogen ions and carbonate ions:



When carbon dioxide is added to seawater, the relative proportions of the carbonic acid complex (dissolved  $\text{CO}_2$  and  $\text{H}_2\text{CO}_3$ ), bicarbonate, and carbonate, shift to maintain charge balance in seawater. This comprises the buffering capacity of seawater to maintain pH. For example, the addition of carbon dioxide to seawater causes an increase in bicarbonate ion concentration, a decrease in carbonate ion concentration, and a decrease in pH. The following

further illustrates the reaction of carbon dioxide and water in the presence of calcium carbonate ( $\text{CaCO}_3$ ) minerals:



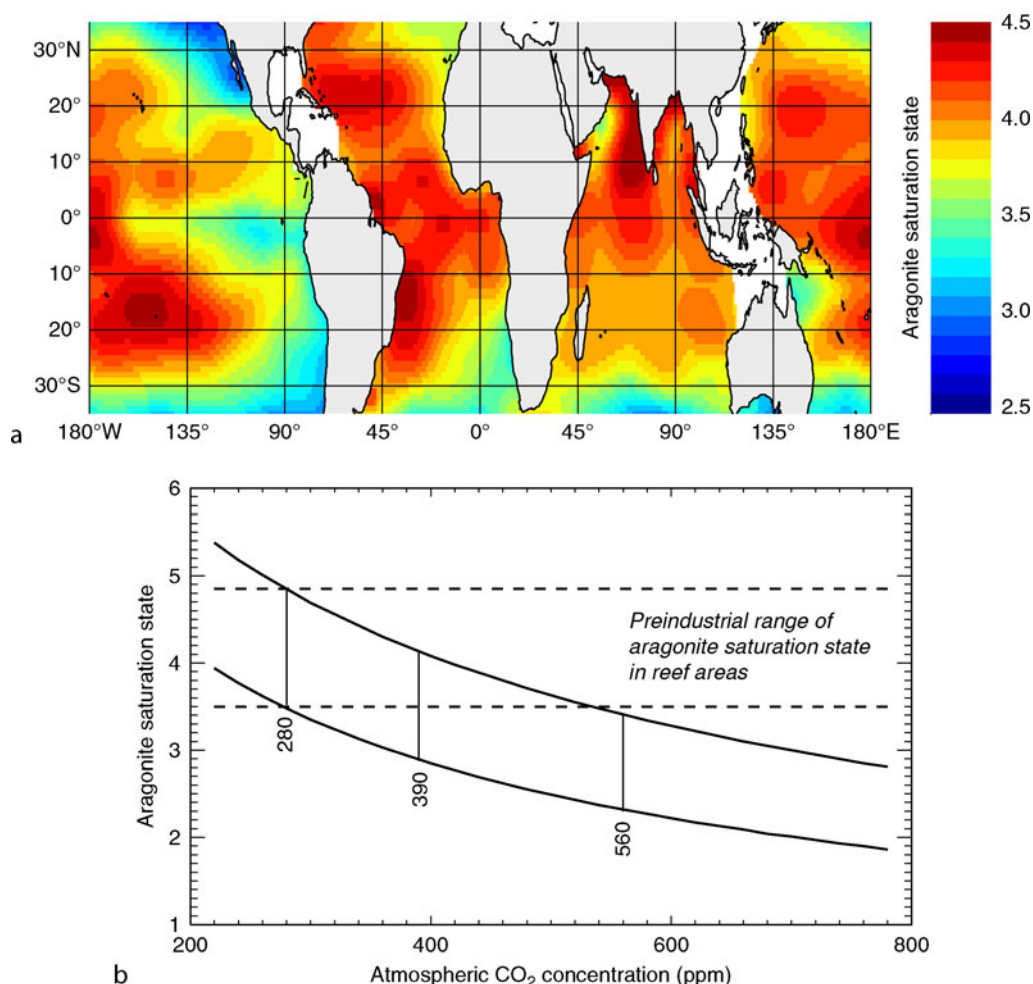
Calcium carbonate production thus releases  $\text{CO}_2$  to the water column while its dissolution removes  $\text{CO}_2$ .

The calcium carbonate saturation state ( $\Omega$ ) is a measure of the ion activity product of  $\text{Ca}^{2+}$  and  $\text{CO}_3^{2-}$  relative to the apparent solubility product ( $K'$ ) for a particular calcium carbonate mineral (e.g., calcite or aragonite). The surface ocean is supersaturated ( $>1$ ) nearly everywhere (Figure 1), but spontaneous precipitation of carbonate minerals is constrained by kinetic barriers. Calcium is much more abundant than carbonate in seawater, so changes in

$\Omega$  mostly reflect changes in the carbonate ion concentration. The calculated  $\Omega_{\text{aragonite}}$  for the tropical oceans, based on a combination of measurements taken in the 1990s (GLODAP, World Ocean Atlas), ranged between about 3.2 and 4.5 (Figure 1a). Most of this variation is due to the 18–30°C temperature range. First order calculations that take into account the progressive increase in atmospheric  $\text{CO}_2$  concentration (with an associated temperature increase) show that aragonite saturation state will decrease to levels outside the preindustrial range (Figure 1b).

### Effects on formation and dissolution of calcium carbonate

Calcium carbonate production in the oceans is almost entirely biogenic, and most is precipitated as one of two



**Ocean Acidification, Effects on Calcification, Figure 1** (a) Aragonite saturation state of tropical oceans estimated by combining  $1 \times 1^\circ$  gridded fields of total alkalinity and total dissolved inorganic carbon normalized to 1990 conditions (GLODAP data base, Sabine et al., 2005) with  $1 \times 1^\circ$  gridded fields of average annual temperature, salinity, phosphate, and silicate (World Ocean Database, 2005; Boyer et al., 2006). Note that these values are highly interpolated and should not be used for research purposes. (b) Aragonite saturation state as a function of atmospheric  $\text{CO}_2$  concentration. Lower and upper solid lines are calculated for 18 and 30°C seawater, respectively, with total alkalinity of  $2,300 \mu\text{eq kg}^{-1}$ , and negligible phosphate and silicate. Parallel dashed lines indicate general range of aragonite saturation state in reef areas prior to the Industrial Revolution. Vertical lines show range of aragonite saturation states at preindustrial atmospheric  $\text{CO}_2$  concentration (280 ppm), the present decade (390 ppm), and 2x preindustrial (560 ppm).

polymorph minerals: calcite, which has a rhombohedral crystal structure; and aragonite, which is orthorhombic. The calcite crystal structure allows some substitution of magnesium ions (Mg) for calcium ions, and calcite with >4 mol%  $\text{MgCO}_3$  is called “high-Mg calcite.” Normally, calcite is much less soluble in seawater than aragonite, but high-Mg calcite with 12–16 mol%  $\text{MgCO}_3$  is about 20% more soluble than aragonite (Morse et al., 2006). Many other factors (impurities, structural disorder) can equally affect the solubilities of calcite, high-Mg calcite, and aragonite.

The saturation states of the various minerals affect the rates of crystallization and dissolution. The rate of calcium carbonate formation, for example, is often expressed as the equation:  $R = k(\Omega - 1)^n$ , where  $k$  is the rate constant and  $n$  the reaction order.

The solubilities of the calcium carbonate minerals have been of interest to Earth scientists for some time, mainly because interpreting Earth’s history requires an understanding of the processes controlling production and preservation of calcium carbonate deposits. Waters of low pH, such as those in the deep sea, have long been known to be corrosive to calcium carbonates, as first noted by Murray and Renard (1891).

Marine calcifying organisms typically precipitate either one mineral or the other, and only a few species have the capacity to precipitate two. In general, calcite secretors (e.g., coccolithophorids) occur in higher latitudes where colder waters can hold more  $\text{CO}_2$  and thus have lower carbonate saturation. Organisms that precipitate the more soluble minerals aragonite (e.g., scleractinian corals) and high-Mg calcite (e.g., crustose coralline algae) are favored in low latitudes, which have higher saturation. Over geologic time, the dominant mineralogy of shallow water carbonates, as well as their preservation potential, has also fluctuated with shifts in seawater carbonate chemistry (Sandberg, 1983). The preferential disappearance of corals and other marine reef-builders in several major extinction events is coincident with rapid ocean acidification (Veron, 2008; Knoll et al., 2007).

### Effects on calcification of marine organisms

Controlled laboratory experiments have provided most of the evidence that ocean acidification will reduce calcification in corals and coralline algae. Results of these experiments indicate that calcification rates of most tropical coral species will decline significantly as ocean acidification proceeds (reviewed in Kleypas and Langdon, 2006; Langdon and Atkinson, 2005). A wide range of responses has been observed, but on average, experimental results under conditions of  $2\times$  preindustrial  $\text{CO}_2$  concentrations fall within two response classes: (1) >40% reduction in calcification rate and (2) <10% reduction (Langdon and Atkinson, 2005). Calcification in newly settled coral polyps may also be impaired at elevated  $\text{CO}_2$  (Albright et al., 2008). There is no evidence yet that corals can adapt to these changes, but the response is reversible

(calcification will increase if pH is increased). The skeletons of some live coral species dissolve completely when placed in waters undersaturated with respect to aragonite, with the coral polyps left in a “naked” or anemone-like state (Fine and Tchernov, 2007). These can re-precipitate skeletons when replaced in waters of normal aragonite saturation. The coral polyps appeared unharmed in these experiments, but naked corals are considered vulnerable in the wild, and would lose their reef-building function.

Experimental results indicate that calcification rates of tropical reef-building coralline algae and rhodoliths respond more strongly to ocean acidification than those of corals, which may be due in part to the high-Mg calcite mineralogy of coralline algae skeletons. Some experiments show net dissolution of coralline algae at atmospheric  $\text{CO}_2$  concentrations as low as 700 ppm (Kuffner et al., 2008; Jokiel et al., 2008; Anthony et al., 2008). The recruitment of tropical crustose coralline algae in experimental mesocosms is also reduced at higher  $\text{CO}_2$  concentrations (Kuffner et al., 2008).

Evidence that ocean acidification is currently affecting reef-building organisms has been difficult to obtain, mainly because of the difficulty in measuring calcification rates over time. Calcification rates derived from coral skeletons of massive *Porites* species indicate a dramatic decrease in calcification beginning around the year 1990 (De’ath et al., 2009), but it is unclear whether this decrease is due to increased temperature, ocean acidification, or a combination of the two.

The effects of decreased calcification on the survival of calcifying reef organisms are not well understood. Some calcifying organisms become absent near a natural submarine  $\text{CO}_2$  vent in a shallow region of the Mediterranean (Hall-Spencer et al., 2008). Calcium carbonate shells and skeletons probably have a protective function, but may also allow organisms to secure themselves to the substrate, compete for space, or optimize light gathering for photosynthesis.

### Effects on coral reef structures

Coral reef structures are produced by the accumulation of  $\text{CaCO}_3$  skeletal debris of corals, coralline algae, and other reef calcifiers. Ocean acidification slows net calcium carbonate production by decreasing carbonate production and/or increasing carbonate dissolution (Kleypas et al., 2001). Dissolution rates of reef sediments increase significantly under elevated  $\text{CO}_2$  conditions, particularly in sediments with a high percentage of high-Mg calcite (Yates and Halley, 2006; Andersson et al., 2007). Monitoring of net community calcification rates on coral reefs (Silverman et al., 2009a) indicate that many or most coral reefs will shift to a state of net dissolution once  $\text{CO}_2$  concentration reaches  $2\times$  preindustrial levels (Silverman et al., 2009b). Other studies suggest that, under elevated  $\text{CO}_2$  conditions, inorganic cementation of coral reef structures is lower, and erosion rates are higher (Manzello et al., 2008). Erosion rates of common microscopic euendolithic



algae that bore into coral skeletons have also been shown to increase dramatically under elevated CO<sub>2</sub> conditions (Tribollet et al., 2009). Decreased calcium carbonate production and increased erosion is likely to reduce architectural complexity of a reef (Alvarez-Filip et al., 2009), and thus may affect reef biodiversity.

### Other effects of ocean acidification on coral reefs

Ocean acidification causes a suite of changes in the carbonate system in seawater, and some of those changes affect other physiological processes in reef organisms. Some corals and coralline algae have been shown to bleach at lower temperature thresholds under lowered pH conditions (Anthony et al., 2008). The olfactory senses of larval orange clownfish *Amphiprion percula* were impaired under lowered pH conditions, which affected their homing ability (Munday et al., 2009). Some organisms, however, may benefit from ocean acidification. Seagrasses, for example, have been shown to increase growth rates from CO<sub>2</sub>-fertilization (Palacios and Zimmerman, 2007).

### Summary

Ocean acidification, a consequence of the ocean's increased absorption of CO<sub>2</sub> from the atmosphere, causes shifts in multiple components of the carbonate system in seawater. One of the best-known impacts of ocean acidification on coral reefs is the reduced rate of calcification in corals and coralline algae. Calcification rates of both groups are expected to decrease significantly with further increases in atmospheric CO<sub>2</sub> concentrations, and dissolution of reef rock and sediments will increase. The direct effects of ocean acidification on organism survival and ecosystem functioning are not well known, but loss of reef habitat and architectural complexity are expected outcomes. Findings from multiple fields of study (paleontology, paleoecology, chemical oceanography, biochemistry, isotope geochemistry, etc.) suggest that ocean acidification will lead to decreased calcium carbonate production, a shift from reef-building toward reef destruction, and reduced biodiversity of reef ecosystems.

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## Cross-references

Algae, Coralline  
 Aragonite  
 Calcite  
 Carbonate Budgets and Reef Framework Accumulation  
 Climate Change and Coral Reefs  
 Corals: Biology, Skeletal Deposition, and Reef-Building  
 Mass Extinctions, Anoxic Events and Ocean Acidification  
 Rhodoliths

## OCEANIC HOTSPOTS

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### Definition

Site occupied by a seamount or oceanic island, usually located away from plate boundaries, where long-lived (>5 Myr), volcanism occurs or has recently occurred.

### Introduction

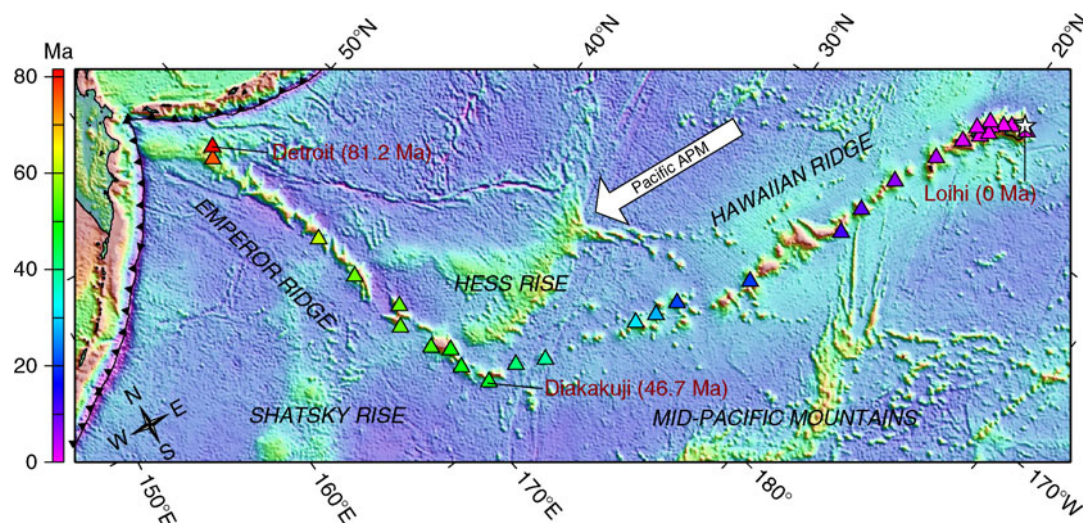
Volcanism occurs mainly at or near active plate boundaries, in particular at mid-ocean ridges. However, there are important exceptions where volcanic activity occurs within plate interiors. In the ocean basins, the prime observational evidence comes from the presence of linear chains of islands and seamounts, sometimes extending for thousands of kilometers across the ocean basins. These island and seamount chains exhibit a general progression of decreasing elevation along the chain from volcanic island to fringing reef, to atoll, and finally to a submerged flat-topped seamount (guyot). An active or dormant volcano usually occupies the young end of an island chain, with progressively older and extinct volcanoes occurring along the rest of the chain. Such topographic features were

suggested to have formed as the plate moved over a relatively stationary “hot spot” in the Earth’s mantle, where an upwelling mantle plume brings hot magma from great depths to the surface (Morgan, 1971; Wilson, 1963). The archetypal example of this process is the Hawaiian-Emperor seamount chain (Figure 1). The mantle plume that produced this ~6,000 km long chain is presently situated beneath the Big Island of Hawaii, the site of active volcanism today. Extending 3,500 km to the northwest lies a linear chain of islands, atolls, and seamounts; there, near the Diakakuji Seamount the chain exhibits a sharp ~60° change in orientation and continues another 2,500 km north-northwest to the Aleutian trench. The age of the volcanism gets progressively older with increasing distance from Hawaii, which is seen as a key observation that validates the hot spot hypothesis. Although predominantly an oceanic phenomenon, hot spot volcanism is not restricted to the ocean basins; volcanism of a similar type occurs within continents, one example being the activity of Yellowstone National Park in the western North America.

### Origin of oceanic hotspots

The hotspot hypothesis states that seamount chains and oceanic islands are the surface manifestation of impinging mantle plumes. These upwelling mantle plumes are thought to originate either at the core-mantle boundary (2,900 km depth) or the boundary between the lower and upper mantle (670 km depth). One theory suggests that a “plume head” develops, above a “plume stem” (e.g., Richards et al., 1989) but other scenarios of plume development with double plume heads (Bercovici and Mahoney, 1994) and time varying magma output (Coffin et al., 2002) have also been considered. As originally proposed (Morgan, 1971; Wilson, 1963), these plumes were considered stationary relative to the lithospheric plates that move over them, but recent evidence suggests that some plumes may have experienced considerable drift over their active lifespan. In particular, deep-sea drilling of seamounts in the northern Emperor seamount chain recovered oriented samples the magnetic memories of which imply that they must have formed at latitudes some 10–15° further north than the present location of the Hawaii hot spot. These systematic discrepancies have led to suggestions that the mantle plume was further north in the past and consequently has drifted south since the formation of these seamounts (e.g., Tarduno et al., 2009).

It is not entirely clear how mantle plumes manage to reach the surface. Apparently weakened by the impinging plume, the lithosphere allows magma to migrate through cracks and fractures and eventually reach the surface. There, a volcano builds upon the surface of the plate directly above the plume. The constant motion of the plate, however, will eventually carry the volcano too far from the source of magma and the volcano becomes extinct. As extinct volcanoes no longer have the



**Oceanic Hotspots, Figure 1** Geometry and ages of the Hawaii-Emperor seamount chain. The major bend in the chain occurred at 47–50 Ma (Sharp and Clague, 2006). Hotspot location (star) is located near Kilauea. Triangles indicate position of samples and their radiometric age is indicated by the color. White arrow shows the approximate Pacific absolute plate motion since ~47 Ma.

regenerative volcanism to combat erosion, they subsequently erode as they cool and subside to form fringing reefs and atolls. With time, they eventually sink below the surface of the sea to form a seamount. Wave action will often flatten the top of such seamounts, leading to the classical truncated guyot (Hess, 1946). As long as the mantle plume supplies heat and magma, new active volcanoes will form directly above the mantle plume and the process continues. Mantle plumes may stay active from a few tens to a few hundred million years.

The relative motion between plates and plumes causes the formation of lines of extinct volcanoes; these exhibit monotonic age progressions and reflect the history of past plate motions. Since the early formulation of the hotspot hypothesis, numerous hotspots have been proposed for sites of unusual volcanic activity (e.g., Burke and Wilson, 1976; Clouard and Bonneville, 2001; Sleep, 1990) yet conclusive imaging of the underlying mantle plumes using seismic tomography remains elusive (Nataf, 2000), perhaps with Iceland (Wolfe et al., 1997) as an exception. For instance, the archetypal strong plume that many believe has formed the Hawaii-Emperor seamount chain and currently thought to underlie the southeast end of the Big Island of Hawaii is not well resolved, whereas other, less productive hotspots (e.g., Easter, Ascension, Azores) appear more dominant in the tomographic images (Montelli et al., 2004). However, recent three-dimensional seismic imaging beneath the Hawaiian Islands now seem to require an upwelling mantle plume (Wolfe et al., 2009). Although the simple age progressions predicted by the hotspot hypothesis are borne out by observations for several seamount chains (such as the Hawaii-Emperor and Louisville chains), others exhibit a more complex age pattern which casts some doubt on the hotspot theory being the only explanation for such volcanism (e.g., McNutt et al., 1997).

### Mantle plumes and hotspot swells

Large bathymetric swells may form around and downstream from the site of active hotspots (e.g., McNutt, 1998). While seamount chains are usually confined within a relatively narrow zone (~100–200 km), the broader effect of plumes on the lithosphere and upper mantle can extend for ~1,000 km or more. Again, the most well-known case of a hotspot swell is associated with the Hawaiian chain where the seamounts are centrally arranged on top of a broad (~1,200 km) swell extending for ~3,000 km (e.g., Van Ark and Lin, 2004). Despite this classic example, similar thermal swells are found in all oceans and always associated with hotspot chains. The amplitude and extent of such swells correlate strongly with the age of the underlying lithosphere; hence Hawaii (located in an area with seafloor of around 100 Ma) is more elevated than similar swells found in French Polynesia where the seafloor is only half that age (Cazenave et al., 1988). The earliest studies of hotspot swells concluded that the shallow bathymetry simply reflected reheating of the entire lithosphere (Detrick and Crough, 1978). However, others have pointed out the likely effect of compositional buoyancy (e.g., Jordan, 1979; Phipps Morgan et al., 1995) and dynamical uplift (e.g., Olson, 1990). In summary, hotspot swells appear to require the presence of a deep-seated upwelling plume as such features can explain both a broad swell and narrowly focused volcanism (e.g., Ribe and Christensen, 1999).

### Intraplate seamounts produced at oceanic hotspots

Seamounts formed by hotspot volcanism can accumulate into the largest seamounts present in the oceans. Specifically, intraplate seamounts built on old (and hence thick



and strong) oceanic lithosphere may in some circumstances attain heights of almost 10 km (measured from the seafloor to the tallest peak on an island). This is the case for Mauna Kea, one of five volcanoes that form the Big Island of Hawaii, which by this definition is the tallest mountain on Earth. Given that the smallest features considered by most geologists to be seamounts are 50–100 m tall, the sizes of observed seamounts span almost three orders of magnitude.

Studies have found that the number of seamounts varies considerably across the oceans and that they tend to form both linear and random constellations. Furthermore, their sizes and distributions provide invaluable information about their origins. Ranging from single-beam echosounder profiles, via multibeam surveys, to satellite altimetry, studies have found that the distribution of seamounts can be reasonably well explained by an exponential or power-law model (e.g., Craig and Sandwell, 1988; Smith and Jordan, 1987; Wessel, 2001). Such models support the observation that most seamounts are fairly small. Extrapolations from the power-law trends obtained for large seamounts suggest that perhaps over 100,000 seamounts of heights  $\geq 1$  km may be present in the oceans. Extrapolating further down to the smallest sizes observed (a few tens of meters) would predict a population over one million. However, sediments will most likely have buried the bulk of those seamounts, considering typical 100–200 m sediment thicknesses in the ocean basins (e.g., Ludwig and Houtz, 1979). Consequently, we find that most of the smallest seamounts reside on young seafloor where the sediment cover is modest or nonexistent.

We do not know why seamount abundances vary spatially. One factor may be the underlying distribution of mantle plumes, which seem to be found in higher numbers beneath plates with the largest seamount abundances. Another factor may be systematic variations in plate stresses. We note that smaller plates are possibly in compression, which could prevent the intrusion of magma. Smaller plates are also less likely to have a directional regional stress dominating the state of stress, and often are relatively young and buoyant (e.g., the Cocos plate); during subduction, such plates would only be associated with slightly negative buoyancy forces. On the other hand, the large Pacific plate, and specifically its equatorial region, appears to be under tension from the slab pull forces at the distant subduction zones, as evidenced by widespread extensional volcanism that is neither associated with hotspots nor mid-ocean ridges (e.g., Sandwell et al., 1995; Wessel and Kroenke, 2007). Finally, plates that move the fastest over the underlying mantle appear to have the highest seamount abundances provided they share at least one spreading plate boundary.

## Summary

Oceanic hotspots are the surface expression of rising mantle plumes from the Earth's interior and are responsible for much of the intraplate volcanism observed in the ocean

basins. Being relatively stationary with respect to the surrounding mantle, the oceanic hotspots produce linear chains of islands and seamounts as tectonic plates move over these sites.

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## Cross-references

[Atolls](#)  
[Plate Tectonics](#)  
[Subsidence Hypothesis of Reef Development](#)  
[Volcanic Disturbances and Coral Reefs](#)  
[Volcanic Loading and Isostasy](#)

## OCTOCORALLIA

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## Synonyms

Alcyonaria (this term is now rarely used). Common names: Gorgonians; Octocorals; Sea fans; Sea pens; Sea whips; Soft corals

## Definition

Octocorallia (also known as octocorals, or in earlier times “Alcyonaria”) are a subclass of the class Anthozoa, in the phylum Cnidaria. They are sessile polyp-bearing animals with a mobile larval phase that are only found in marine systems. The distinguishing characteristic of this subclass is that their polyps always bear eight tentacles (hence octocoral), which are usually (but not always) fringed along both edges by one or more rows of pinnules. The gastro-vascular cavities are typically subdivided by eight septa.

## Introduction

Octocorals are a major component of the sessile benthic fauna of many coral reefs. Like Scleractinian corals, they are modular (colonial) organisms which develop through asexual replication and specialization of polyps. In contrast to Scleractinian corals (the primary reef building corals), most octocorals do not usually deposit a rigid calcium carbonate exoskeleton, and they therefore tend to attach to reefs rather than contribute substantially to their framework or to sedimentary deposits. However, there are a number of exceptions that do contribute substantially to framework accretion, sedimentary deposits, and sediment stabilization (see below).

## Classification

Octocorallia are a subclass of the class Anthozoa, phylum Cnidaria. Like other anthozoans, octocorals bear polyps that consist of a tubular body, terminating in a mouth that is surrounded by hollow tentacles. Unlike other anthozoans, octocoral polyps always bear eight tentacles, which are usually fringed by rows of pinnules. Polyps are internally compartmentalized by eight mesenteries. The ectoderm of the tentacles contains simple nematocysts (cnidae or stinging cells) that are unable to paralyze large zooplankton or sting other larger animals. The ectodermal and endodermal cell layers are often connected by a relatively thick and cellular mesoglea, which often contains calcium carbonate sclerites and collagen. Most octocorals are colonial, with the exception of one deep-water species with a single solitary polyp (*Taiaroa tauhou*). A colony develops from a single founder polyp by asexual propagation (polyp budding). The resulting multiple polyps in a colony are often embedded into coenenchymal tissue, but remain connected by canals (solenia).

There is substantial taxonomic uncertainty associated with Octocorallia. At present, the subclass is divided into three orders ([Figure 1](#)):

- Helioporacea
- Pennatulacea (sea pens)
- Alcyonacea (soft corals and gorgonians)

The Helioporacea are represented by a single species, the blue coral, *Heliopora coerulea* (family Helioporidae) in the Indo-Pacific, and the genus *Epiphaxum* (family Lithotelestidae) in the Caribbean. *H. coerulea* has no calcium carbonate sclerites, instead colonies consist of a massive aragonite skeleton perforated by wide cylindrical cavities containing the polyps, connected by narrow solenial tubes.

The Pennatulacea (sea pens) presently distinguish around 200 species in 32 genera (15 families; Williams, 1995, 1999). The body of pennatulaceans consists of a single large primary polyp, called the oozoid, with a basal fleshy peduncle for anchorage in soft substratum. Through lateral budding of the upper body wall of the oozoid (rachis), two types of secondary polyps are being



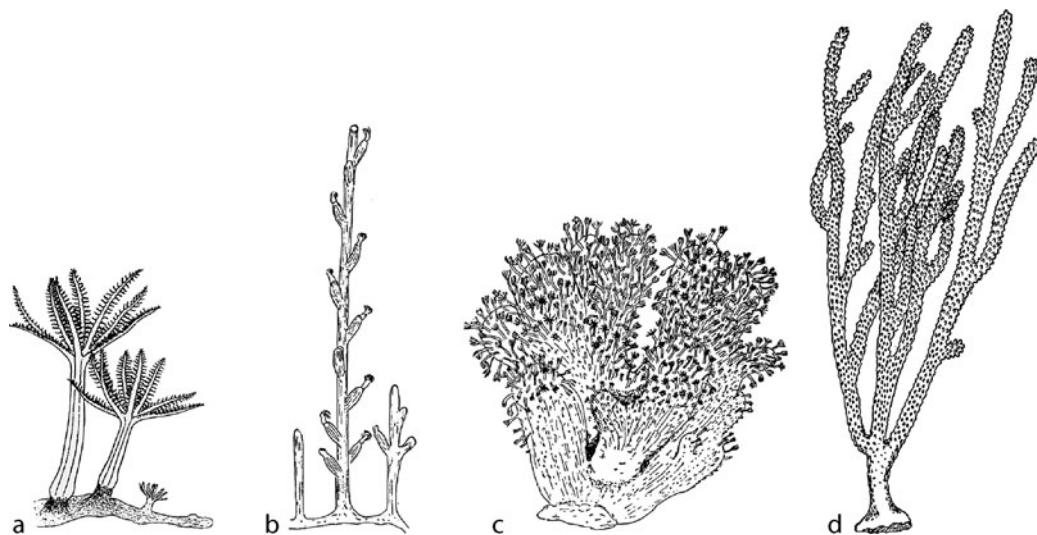
**Octocorallia, Figure 1** Representatives of the three orders of Octocorallia: (a) Helioporacea; (b) Pennatulacea; (c and d) two common morphological groups of Alcyonacea, soft corals, and gorgonians.

formed, autozooids and siphonozooids, with mesozooids as an additional third type of polyps in a few taxa. Pennatulaceans typically live in soft bottom habitats, being completely retracted during the day and emerging in the dark. The greatest pennatulacean diversity is found in the tropical Indo-Pacific (nine genera in five families).

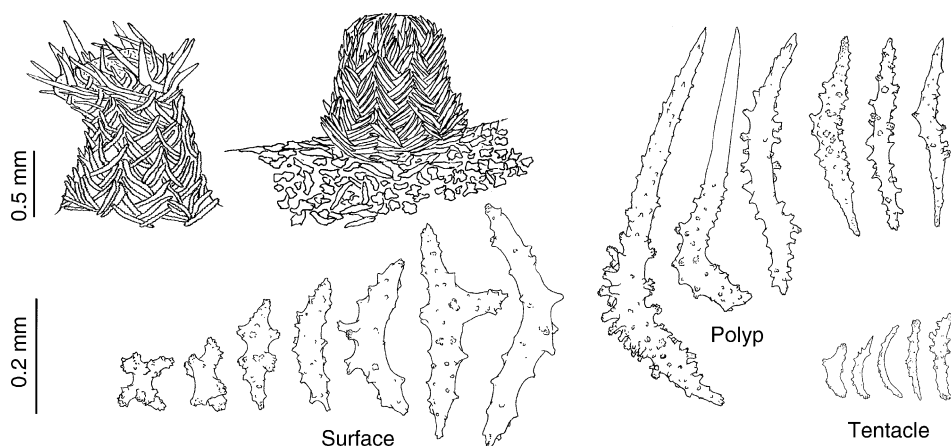
The Alcyonacea (soft corals and gorgonians) contain the large majority of octocoral species. The number of species is unknown, as numerous species await taxonomic

description and many genera need urgent revision. In shallow tropical and subtropical Indo-Pacific reefs alone, about 100 alcyonacean genera in 23 families are currently described (Fabricius and Alderslade, 2001). Their growth forms range from small colonies with few polyps connected by stolons, to fleshy soft corals to up to 3 m large sea fans (Figure 2). Within the order Alcyonacea, the term “soft coral” is commonly used to only refer to octocorals without internal axis or solid skeleton. In





**Octocorallia, Figure 2** Representative morphological groups of alcyonacean octocorals: (a) single polyps connected by stolons; (b) tall axial polyps that bud off lateral polyps; (c) polyps embedded in a fleshy tissue mass ("soft coral"); (d) gorgonian sea fan with upright growth form and internal axis (modified from Hyman, 1940).



**Octocorallia, Figure 3** A representative set of octocoral sclerites of the genus *Acanthogorgia*. Sclerites are the main feature used for taxonomic analyses (drawing by P. Alderslade, from Fabricius and Alderslade, 2001).

contrast, the terms gorgonian, sea fan, sea rod, or sea whip are generally used to refer to octocorals that arise from the substratum with the support of an internal axis (but excluding sea pens and blue coral). However, in the Caribbean where gorgonians dominate the octocoral fauna, the term soft coral is often used for all octocorals. While the terms soft coral and gorgonian continue to be used to differentiate between morphological groups (and continues to be used in some classification schemata), continua of intermediate forms exist, and earlier taxonomic separations of the Alcyonacea into different groups have been abolished by most classifications (Bayer, 1981). Phylogenetic research suggests that further significant changes to the current classification may be warranted.

Most octocoral colonies are supported by sclerites embedded in the tissue, and a hydroskeleton or a proteinaceous and/or calcareous axis. Sclerites are minute calcareous structures typically less than 0.3 mm in length (range about 0.02 to >12 mm; Figure 3). Some species have neither sclerites nor other calcareous structures (e.g., some Xenidae). A few species (e.g., *H. coerulea*, *Tubipora musica*, and *Corallium*) have a solid skeleton. The rigid structure of these species contributes to habitat complexity on the reef during their life, and they may also contribute to reef framework and sedimentary deposits on their death. Some species of *Simularia* also contribute to reef structure and sediment stabilization by depositing massive trunks of consolidated sclerites that can reach decimeters across and meters in height.

Among the gorgonians, a wide variety of additional supporting structures are found. Their internal axes may consist of fused or unfused sclerites, sometimes bound by amorphous calcareous material, solid calcium carbonate, and/or a combination of collagen and gorgonin (a dark, hard proteinaceous material related to horn). For example, sections along the axis may alternate between horny and calcium carbonate materials (family Isididae), nodes and internodes (family Melithaeidae), or layers across the axes may consist of a gorgonin core surrounded by large amounts of calcareous material (family Ellisellidae). The shape and size of sclerites, the structure and material composition of the internal axes, and colony growth forms are the main features used for taxonomic analyses (Fabricius and Alderslade, 2001). Sclerites may be investigated by placing a small amount of tissue (1–3 mm<sup>3</sup>) onto a microscopic slide, and digesting the tissue with a few drops of concentrated bleach (sodium hypochlorite). Once the tissue is digested and bubble formation has ceased after a few minutes, a few drops of a glycerol and cover slip are applied for casual microscopic examination. To produce permanent slides, the sclerites are rinsed in freshwater and then in 95% ethanol. When all liquid is completely evaporated and the sclerites dry, an acid-free mounting medium and a cover slip are applied.

### Evolution and biogeography

Due to a lack of preservable features, very little is known about the evolution of octocorals. The Pennatulacea are an exception, with phylogenetic analyses presented by Williams (1993a, 1995). Williams postulates that the Pennatulacea as a group initially differentiated from shallow-water alcyoniid-like ancestors in the shallow waters of tropical oceans, and subsequently diversified and dispersed to all depths of the temperate and polar regions, as well as the tropics. The most primitive pennatulacean group Veretillidae show a range of similarities with some alcyonacean taxa, and like the alcyonaceans are most diverse in the Indo-Pacific at <100 m depth. Highly derived forms such as *Virgularia* and *Pteroeides* are sympatric with the more primitive taxa in the shallow-water tropics, while other highly derived forms such as *Chunella* and *Umbellula* are restricted to deep water. Some pennatulacean fossils date back to the Mesozoic.

There are still major gaps in the understanding of octocoral biogeography. In Indo-Pacific coral reefs, detailed octocoral studies include those from New Caledonia (Grasshoff, 1999), the Great Barrier Reef (Fabricius and De'ath, 2008), Japan (Benayahu, 1995), Palau, Micronesia (Fabricius et al., 2007), and South-Eastern Africa (Williams, 1993b; Benayahu et al., 2003). Despite the sparsity of available information, it appears likely the center of biodiversity for shallow-water reef-inhabiting octocorals coincides with that of other reef inhabiting organisms, namely the "Coral Triangle" that includes

Indonesia, Malaysia, and the Philippines. Very little taxonomic overlap exists between the Caribbean and the Indo-Pacific octocoral fauna.

### Biology and ecology

Octocorals include a moderately diverse range of species with widely contrasting biological properties. Life expectancy and growth rates of most soft corals and gorgonians are largely unknown. Being modular organisms, the relationship between colony size and age is weak, as colonies may show negative growth when torn by storm waves or damaged by moving rubble or predation.

After hard corals, octocorals are the second-most common group of macrobenthic animals on many Indo-Pacific and Caribbean coral reefs. On the Great Barrier Reef, octocoral cover averages 3–35% on outer reef slopes, but may be up to 70% in current-swept yet wave-protected environments such as channels between reefs or islands (Fabricius and De'ath, 2008).

Dispersal strategies vary greatly among species, and include asexual propagation and sexual reproduction. Asexual propagation may be based on the generation of daughter colonies at the terminal ends of stolons, or the budding of miniature colonies that fall of the mother colony and settle near-by. Fragmentation also occurs when a central section of a colony dies yet the edges survive and reorganize into complete colonies. Two modes of sexual reproduction exist: first, in "broadcasting" species the male and female gametes are released into the water column. After fertilization, the pelagic larvae are dispersed by currents until they settle some days to weeks later. Second, in "brooding" species the eggs are fertilized on or within the mother colony, and the resulting larvae develop on the colony surface until they detach and settle nearby some days later.

Despite being sessile and not having a protective skeleton, overall feeding pressure on octocorals appears remarkably low. The few known species to predate upon octocorals include some snails (e.g., the cowry shell *Ovula ovum*), nudibranchs, fish (e.g., the butterfly fish *Chaetodon melannotus*), and there is occasional grazing by young green sea turtles (*Chelonia mydas*) and echinoderms such the sea urchin *Diadema*. Many octocorals are effectively protected against predation, fouling by algae or overgrowth by neighboring organisms through feeding-deterrent, toxic, or allelopathic secondary metabolites. Some of these substances appear to be of pharmaceutical or bioactive value.

A range of epibenthic organisms are associated with octocorals. Amphipods are commonly found in large numbers on octocoral colonies, and some species of brittle star (Ophiuroidea), feather star (Crinoidea), shrimps, barnacles, ctenophores, and fish (gobies and pygmy sea horses) are exclusively found on the surface of some octocoral taxa. Most of these associates use the octocoral colony as a perch or for shelter; however, some of the epibenthos also appear to feed on octocoral mucus.

Octocorals are passive suspension feeders that filter particles from the water column, relying on currents to carry the food particles toward their polyps (Best, 1988; Fabricius et al., 1995; Ribes et al., 1998). Much of the food is therefore derived from phytoplankton, minute detrital particles, flagellates, and very small zooplankton: their simple stinging cells are unable to capture larger zooplankton. In addition, endosymbiotic algae (genus *Symbiodinium*, historically also called zooxanthellae) are found in about half of the Indo-Pacific reef-inhabiting octocoral taxa, and in most Caribbean octocorals. Zooxanthellae supply photosynthetically fixed carbon to the host, while the host in return provides nutrients and shelter to the algae. This finely tuned symbiosis between animal and alga depends on the availability of light for photosynthesis. Symbiotic (zooxanthellate or phototrophic) taxa include many representatives within the “true” soft corals (the Alcyoniina group), especially within the abundant families Nephtheidae, Alcyoniidae, and Xenidiidae, but also most Caribbean gorgonians (van Oppen et al., 2005). In contrast, most Indo-Pacific sea fans, and also several soft coral genera (e.g., *Dendronephthya*) do not contain zooxanthellae. These asymbiotic (azooxanthellate or heterotrophic) taxa are visually distinguished from their phototrophic relatives, which are typically brown, beige, or cream in color (Figure 1a, c), by their bright yellow, orange, red, pink, purple, or snow-white coloration (Figure 1b, d). Throughout their evolutionary history, groups of octocorals have repeatedly entered into and lost their association with endosymbionts (van Oppen et al., 2005).

The diversity of an octocoral community at a given site depends on three factors. First, the biogeographic location and colonization history of a region determines the regional species pool present. The diversity of octocorals in coral reefs strongly attenuates with latitude, and with distance away from the “coral triangle.” Second, environmental conditions determine what subset of the local species pool occurs at that locality. Abundances of particular taxa are strongly determined by the physical environment, especially light availability and water currents, which are both related to energy availability (Fabricius and De'ath, 2008). Azooxanthellate taxa are mostly found in low-light and high-flow environments, while zooxanthellate taxa require high light levels and relatively clear water. Azooxanthellate taxa tend to have lower abundances and more restricted geographic ranges than their zooxanthellate relatives, hence energy gains from symbiosis contribute to high local species richness in clear-water reef environments (Fabricius and De'ath, 2008). Third, at any point in time local and regional species richness also depend on disturbance history, specifically the nature and intensity of the disturbance, and the time since past disturbances have removed colonies. Major disturbances of octocoral communities are those from storms (with storm waves tearing off and damaging colonies), episodes of high water temperatures (leading to bleaching and mortality of zooxanthellate taxa), chronically reduced water clarity

(reducing photosynthesis), and high sedimentation events (smothering colonies or hampering larval settlement).

### Threats and conservation issues

Few octocorals are exploited for human use. Exceptions are *Tubipora* spp. (organ pipe coral) and *H. coerulea* (blue coral), the permanently brightly colored skeletons of which are used for ornaments and jewellery. They are also popular as aquarium species, and the trade of both species is regulated by the Convention on International Trade in Endangered Species (CITES). However, illegal collection of *Tubipora* spp. is wide-spread and in some regions this genus has become rare due to overharvesting.

Octocoral species are affected by the same threats that affect coral reefs globally, in particular climate change, poor land management, and destructive fishing methods. Like hard corals, most octocorals that contain zooxanthellae are highly susceptible to bleaching at high seawater temperatures, and many octocorals have been killed by previous mass bleaching events in many parts of the world. Some sea fans are also highly susceptible to diseases, especially when stressed from high temperatures and/or high nutrient exposure (Ward et al., 2007). Many taxa are also highly sensitive to exposure to increased turbidity, sedimentation, and eutrophication. High turbidity reduces the diversity of zooxanthellate taxa, but has little effect on the diversity of azooxanthellate octocorals (Fabricius and McCorry, 2006), suggesting that octocoral diversity is controlled by energy available for photosynthesis (Fabricius and De'ath, 2008). Macroalgal dominance from eutrophication and overfishing also negatively affect octocoral abundances and biodiversity.

### Summary/Outlook

With their bright colors and diverse sizes and shapes, octocorals greatly contribute to the stunning beauty of coral reefs. Despite their abundance and visual appeal, the taxonomy, phylogeny, biology, and ecological roles of octocorals remain insufficiently understood. Despite these large knowledge gaps, it is undisputed that any measure taken to safeguard the reefs' hard corals will also be effective to protect octocorals as well as the numerous other invertebrate and vertebrate species that inhabit the World's coral reefs.

### Acknowledgments

Many thanks to Phil Alderslade for improving the manuscript.

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## Cross-references

Corals: Biology, Skeletal Deposition, and Reef-Building  
 Corals: Environmental Controls on Growth  
 Nutrient Pollution/Eutrophication  
 Reef Interconnectivity/Larval Dispersal  
 Scleractinia, Evolution and Taxonomy

Sediment Dynamics  
 Sediments, Properties  
 Symbiosis; Zooxanthellae  
 Tropical Cyclone/Hurricane

## OIL AND GAS RESERVOIRS AND CORAL REEFS

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## Synonyms

Carbonate buildup reservoir; Coral reef reservoir; Reef buildup reservoir

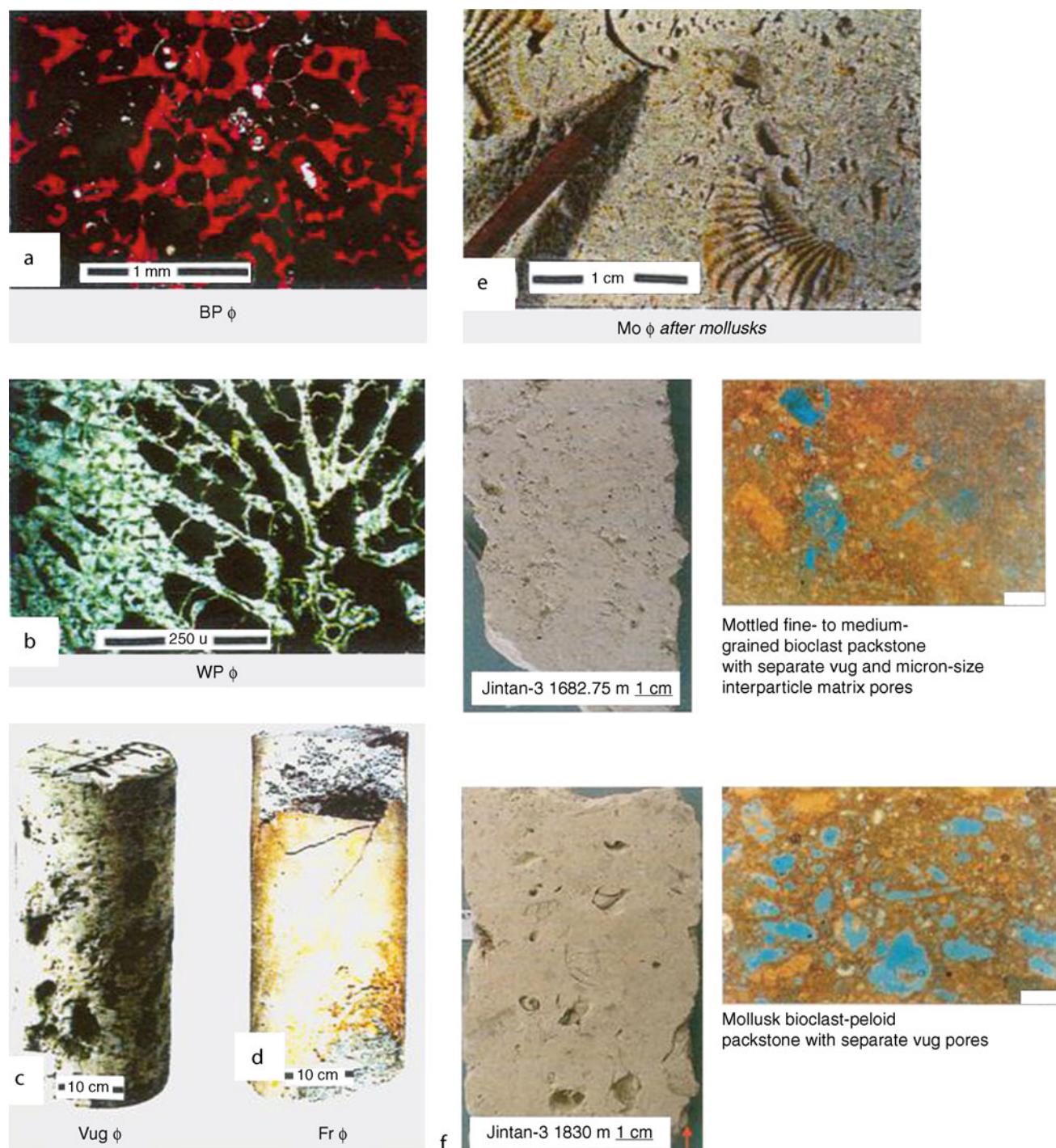
## Definition

Coral reef reservoir: A subsurface volume of coral reef boundstone and associated skeletal grainsupportstone (i.e., packstone–grainstone) that has sufficient porosity and permeability to permit the accumulation of crude oil or natural gas under adequate trap conditions.

## Reservoir characteristics of coral reef systems

Carbonate reservoirs are important contributors to world oil and gas production and contain more than one-half of global discovered, recoverable hydrocarbons (Roehl and Choquette, 1985). Reef and reef-related deposits comprise a significant proportion of these reservoirs, most prominently in carbonate systems of Siluro-Devonian, Cretaceous, and Neogene age. The Neogene-aged reservoirs are commonly composed of coral reef and their associated deposits. In general, the original textures of the carbonate sediments and their early diagenetic pathways are determinants of the likelihood and extent of carbonate reservoir rocks. Primary sedimentary textures related to depositional environment, provide the initial matrix pore system and generally determine the extent of the prospective reservoir. The vast majority of the carbonate reservoirs have undergone modification of primary pore space because of syn- to post depositional diagenesis. Both occlusion and enhancement may occur. Preservation of reservoir-quality pore systems is most commonly the result of cessation of occluding processes such as cementation (i.e., early marine, meteoric phreatic, and/or burial), and compaction, rather than the result of pore enhancement from processes like karst solution or dolomitization, although these can be important processes locally and during certain time periods (e.g., icehouse times).

Coral reef and related reservoir-prone deposits are most commonly comprised of thick to massive bedded, reef boundstones in platform margin and platform interior patch reef settings and skeletal rudstones, floatstones, grainstones, and packstones interbedded with the boundstones and in fore-slope debris. Reef deposits occur over relatively small areas (square kilometers to 10s of square kilometers), and range in thickness from meters to



**Oil and Gas Reservoirs and Coral Reefs, Figure 1** Common reef and reef-associated pore types. (a) Interparticle porosity (BP) (bright red) in skeletal grainstone. (b) Intraparticle porosity (WP) in a Pleistocene coral. (c) Vuggy (Vug) porosity in a core from Arun Field. (d) Fracture porosity (Fr) in a core from Rainbow Field (Devonian). (e) Moldic porosity (Mo) after mollusks. (f) Skeletal packstone displaying BP, Vug, and Mo porosity (blue), Jintan Field (Miocene). Molds after gastropods and bivalves, Vugs solution enlarged, irregular holes.



100s of meters (up to a 1,000 m or more), and can have very thick oil columns. The most common depositional pore types in reefs and reef associated beds include interparticle, intraparticle, and growth-framework shelter porosity (see Choquette and Pray, 1970; Lucia, 1999; Lónóy, 2006 for pore classifications) (Figures 1 and 2). These pores generally range in size from mesopores (50–100  $\mu\text{m}$ ) to macropores (>100  $\mu\text{m}$ ), and can have a patchy (e.g., shelter and intraparticle) to uniform (e.g., interparticle) distribution (Lónóy, 2006). Where affected by karst dissolution, pore types include moldic macropores (>30–30  $\mu\text{m}$ ), vugs, and solution-enlarged fractures. Porosity values range from low (<5%) to high (>30%), as does permeability (<100 md to Darcy's). Reef reservoirs are generally very heterogeneous. Porosity ranges from patchy to uniform distribution over moderately large areas, resulting in variable interconnectivity and in many fields, tortuous fluid pathways. Nevertheless, these reservoirs are some of the most prolific in the world (Trice, 2005).

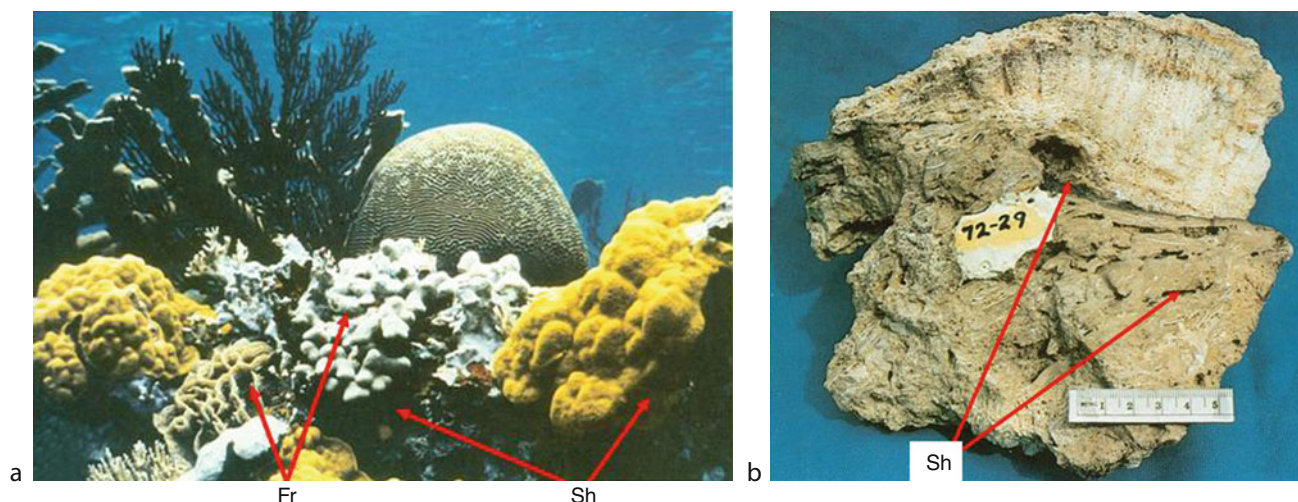
### Reef reservoirs and climate

Climate is a major controlling factor on early diagenesis and pore system history. Greenhouse and icehouse climatic conditions effect carbonates differently (Read, 1995; Trice, 2005). Greenhouse times are characterized by widespread flooding of continental shelves, and by low amplitude sea level changes, typically from 10 to 50 m (Goldhammer et al., 1990; Koerschner and Read, 1989; Wright, 1992; Read, 1995). Greenhouse reservoirs develop in reef and carbonate sand shoal lithofacies that stack in aggradational or gently prograding ramp geometries. Reservoirs are relatively homogeneous, and form extensive sheets. Vertical communication through pore systems is dominated by primary porosity. Small sea level

falls prevent significant drops in water tables, and reduce meteoric diagenetic effects. Long-term exposure (100s kyr) at sequence boundaries can be more significant, and can lead to enhanced meteoric diagenesis, soil formation, and/or silcrete/caliche caps that provide reservoir baffles and barriers. Reef reservoirs of Devonian and Cretaceous age exhibit many of these characteristics.

Ice-house times are characterized by high amplitude (60–100+ m), high frequency sea level fluctuations. Carbonate productivity can vary over short distances, resulting in considerable lateral variability in thickness and internal facies distribution. Deeper muddy subtidal facies, shallow shoal water grainy facies, and facies exhibiting subaerial exposure may be juxtaposed over short lateral distances. High-frequency cycles show juxtaposition of deep water muds, shallow water facies, and subaerial emergence features (Read, 1995), resulting in vertical baffles and barriers to flow. In arid settings, caliche or silcrete will form extensive nonporous caps to depositional cycles. Ice-house reservoirs thus can be more compartmentalized than greenhouse reservoirs.

Icehouse conditions will produce disconformity bounded sequences, 10–100s m thick. High amplitude, sea level fluctuations are significant and cause large-scale lateral and vertical migration of diagenetic zones. Facies deep within platforms are subjected to repeated interaction with marine and meteoric fluids in vadose and phreatic environments. The extent of karst formation is dependent on the climatic conditions at the time of exposure (Perkins, 1977; Beach, 1982). Humid conditions lead to considerable leaching of less stable carbonate minerals (i.e., aragonite and hi-Mg calcite) forming significant secondary porosity (i.e., molds, vugs, caves, caverns, etc.) (Loucks, 1999). Arid settings tend to allow preservation of original primary porosity.

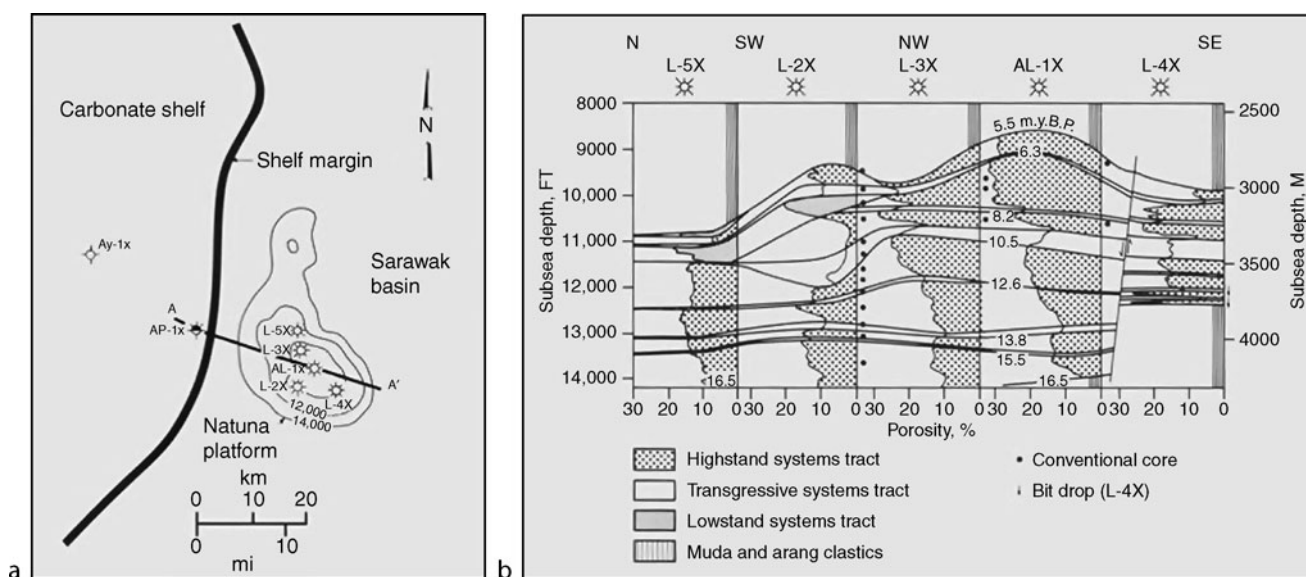


**Oil and Gas Reservoirs and Coral Reefs, Figure 2** Common reef pore types. (a) Living corals, Bahamas displaying abundant potential framework (Fr), and shelter (Sh) porosity. (b) Reef limestone (circa 9,000 years old), Belize. *Montastraea cavernosa* colony on top, underlain by platey algae (*Halimeda*)-rich lime wackestone/packstone. Numerous cavities are dominantly shelter voids (Sh) (scale in cm) (from James, 1983).

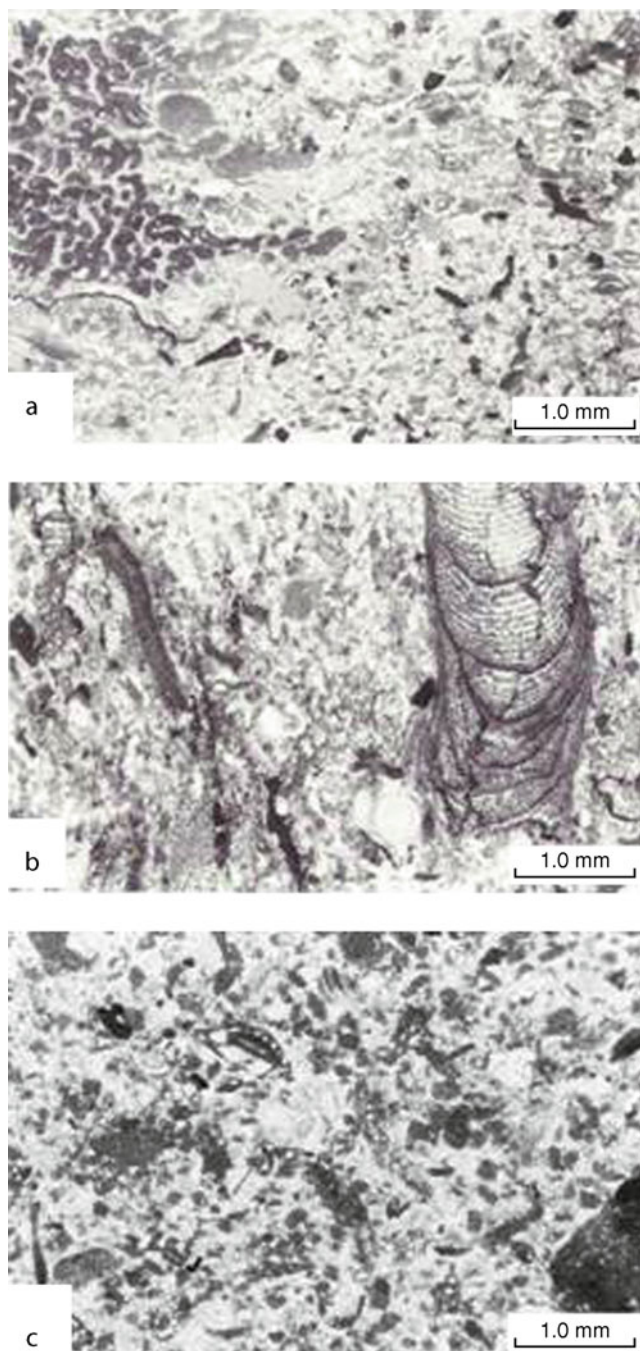


**Oil and Gas Reservoirs and Coral Reefs, Table 1** A partial list of significant Miocene-aged, coral reef platform oil and gas fields, compiled from various sources, including references above (MMBOE million barrels of oil equivalent) (Pore types: *Vug* vuggy, *Mo* moldic, *Chalky* chalky microporosity, *BP* Interparticle, *WP* intraparticle, *Fr* fracture, *BC* Inter-crystalline, *Ch* channel, *Cav* cavernous). Depositional components and pore types listed in order of abundance

| Field name   | Country   | Depositional component               | Porosity types           | Estimated porosity range (%) | Estimated ultimate recovery (MMBOE) |
|--------------|-----------|--------------------------------------|--------------------------|------------------------------|-------------------------------------|
| Arun         | Indonesia | Coral/algal/foram/molluscs           | Chalky, Vug, Mo, WP, Fr  | 5–25                         | 3,900                               |
| Kampung Baru | Indonesia | Coral/algal/foram/molluscs           | Mo, Vug, Chalky, Fr      | 25–30                        | 90                                  |
| Krisna       | Indonesia | Coral/algal/foram/molluscs           | Vug, Mo, Chalky, Fr      | 10–35                        | 55                                  |
| Lho Sukon A  | Indonesia | Coral/algal/foram/molluscs           | Vug, Mo, Chalky          | 5–20                         | 85                                  |
| Liuhua       | China     | Coral/algal/foram                    | Vug, Mo, BP, WP, Chalky  | 15–35                        | 115                                 |
| Nido         | Indonesia | Coral/algal/foram                    | Vug, Mo, Fr              | 1–10                         | 20                                  |
| NSO A        | Indonesia | Coral/algal/foram/molluscs           | Vug, Mo, Chalky, Cav, Fr | 15–30                        | 245                                 |
| Natuna L     | Indonesia | Coral/algal/foram/molluscs           | Vug, Mo, BP, WP, Cav     | 10–30                        | 26,250                              |
| Luconia F6   | Malaysia  | Coral/algal/foram/molluscs           | Vug, Mo, BP,             | 5–35                         | 740                                 |
| Salawati A   | Indonesia | Coral/algal/foram/bryozoan/molluscs  | Vug, Mo, Fr, BC          | ~15                          | 20                                  |
| Kasim        | Indonesia | Coral/algal/foram/bryozoans/molluscs | Vug, Mo, BC, Fr          | 5–40                         | 60                                  |
| Walio        | Indonesia | Coral/algal/foram/bryozoans/molluscs | Vug, Mo, BC, Fr          | 5–30                         | 200                                 |
| Rama         | Indonesia | Coral/foram                          | Chalky, Vug, Mo, BP, WP  | 15–40                        | 125                                 |
| Bima         | Indonesia | Foram/molluscs/coral/algal           | Vug, Mo, Chalky, WP      | 20–40                        | 90                                  |
| Ramba        | Indonesia | Foram/coral                          | Vug, Mo, Chalky, Ch, Fr  | 5–30                         | 90                                  |
| Bombay High  | India     | Coral/algal/foram                    | Vug, Mo, Chalky, Fr      | 15–25                        | 5,015                               |
| Ras Fanar    | Egypt     |                                      | Vug, Mo, Chalky, BC, Fr  | 10–30                        | 140                                 |



**Oil and Gas Reservoirs and Coral Reefs, Figure 3** (a) Natuna L subsea depth structure in feet (from Eyles and May, 1982). (b) Natuna sequence stratigraphy showing well correlations. Platform consists of alternating thick shallowing upward highstands (increasing porosity) (i.e., highstand systems tracts) and thin deepening upward transgressive (decreasing porosity) deposits (i.e., transgressive system tracts). Highstand deposits show porosity enhancement beneath subaerially exposed sequence boundaries (i.e., age date surfaces) (modified after Rudolph and Lehmann, 1989).



**Oil and Gas Reservoirs and Coral Reefs, Figure 4** Thin section photomicrographs of Natuna reservoir lithofacies, plane-polarized light. (a) Coral-red algae boundstone in a grainstone matrix. A moldic, mud-filled coral encrusted by red algae to left. Light gray areas are moldic and vuggy porosity. (b) Coral-red algae-echinoderm packstone/grainstone. (c) Coral-red algae-echinoderm grainstone. Moldic porosity shown in light gray areas (modified after Rudolph and Lehmann, 1989).

The lack of meteoric water allows primary pores to remain open and allows preservation of permeable networks. The Neogene reef reservoirs of the Australasian region are characterized by humid karst-modified primary pore systems. Because of their similarities to Pleistocene and Modern reef systems (Melim et al., 2001) and their significance as oil and gas reservoirs, they are summarized below.

### Neogene reef platform oil and gas reservoirs

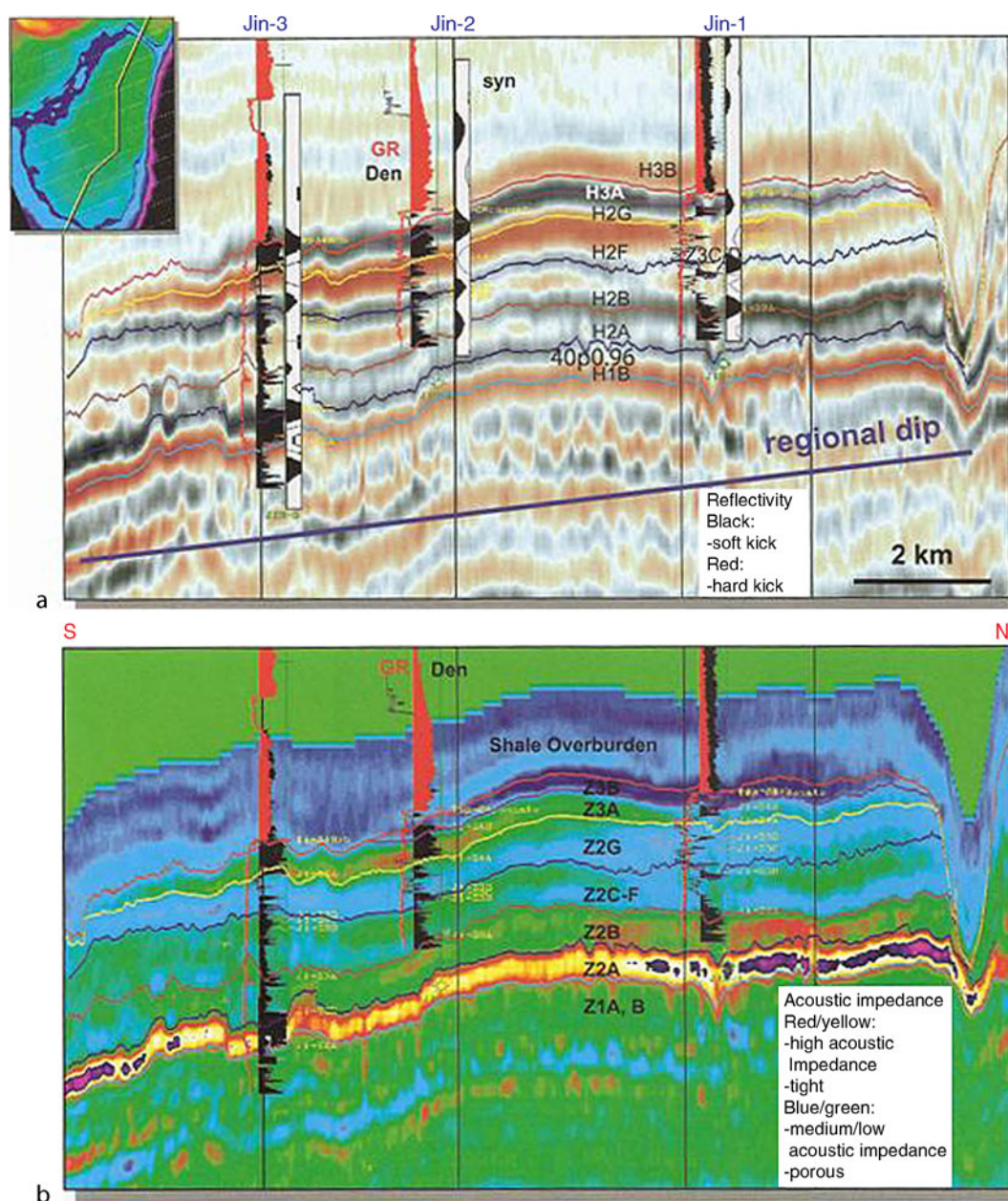
The late Oligocene through Miocene was a period of widespread coral/algal carbonate platform development in the Australasian region (Epting, 1980; Fulthorpe and Schlanger, 1989; Ehrlich et al., 1993; Saller et al., 1993; Gucci and Clark, 1993; Sun and Esteban, 1994). These Neogene reef platforms have been the targets of hydrocarbon exploration and there have been numerous discoveries (Table 1) [i.e., Malaysia: central Luconia (Ho, 1978; Epting, 1980, 1989; Sulaiman, 1995); Philippines: Nido (Withjack, 1985) and Malampaya (Grötsch and Mercadier, 1999); Indonesia: Arun (Abdullah and Jordan, 1987; Jordan and Abdullah, 1992), northwest Java Sea (Yaman et al., 1991); Ramba (Longman et al., 1987); South Lho Sukon (Maliki and Soenarawi, 1991), Natuna (May and Eyles, 1985; Rudolph and Lehmann, 1989); China: Liuhua, Pearl River (Moldovanje et al., 1995)].

Two of these fields, Natuna L (Rudolph and Lehmann, 1989) (Figures 3 and 4), and Jintan, Luconia Province (Vahrenkamp et al., 2004) (Figure 5) illustrate aspects coral reef reservoir architecture and lithofacies. Both of these field examples are isolated reef platforms of middle to late and middle Miocene age, respectively. Reservoir columns are approximately 300 (Jintan) to 1,000 (Natuna) meters in thickness. Reservoir lithofacies range from coral-algal boundstones, rudstones, floatstones, grainstones, and packstones (Figures 1 and 3). Bioclasts also include abundant foraminifera, mollusks, and echinoderms. Porosity ranges from 5 to 40%, and pore types are dominantly Vug, Moldic (Mo), and Interparticle (BP). Each platform has undergone periodic and significant sub-aerial exposure leading to secondary porosity enhancement (Figures 3 and 4). The best reservoir quality occurs in highstand systems tract deposits that have been subjected to subaerial exposure. These reservoirs tend to stack vertically and extend across each platform (Figures 3 and 5).

### Summary

Carbonate reservoirs are important contributors to world oil and gas production (>50% of global reserves), and reef reservoirs are a significant proportion of these reservoirs. They are particularly abundant in the Siluro-Devonian, Cretaceous, and Neogene time periods. The Neogene-aged reservoirs are commonly coral reef and associated





**Oil and Gas Reservoirs and Coral Reefs, Figure 5** (a) Reflection and (b) acoustic impedance section through Jintan field. Synthetic seismic logs show good match with seismic. Horizons (H1B, H2A, etc.) define reservoir zones shown on acoustic impedance (Z1a, Z2a, etc.). Low impedance areas (blue/green) (i.e., higher porosity) show both vertical and lateral connectivity (from Vahrenkamp et al., 2004).

grainsupportstone deposits. Reef reservoir pore systems are generally characterized by some combination of primary depositional, and diagenetic pore types. Porosity ranges from patchy to uniform, resulting in vertical and horizontal heterogeneity. Climate controls the effects of early diagenesis. Greenhouse reservoirs show less effect of subaerial dissolution and greater internal continuity. Icehouse reservoirs that have been affected by humid karst conditions show significant pore system modification. The Neogene coral/algal

reservoirs are most similar to modern reef systems and exhibit dissolution modification of their pore systems.

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## Cross-references

Diagenesis  
 Density and Porosity: Influence on Reef Accretion Rates  
 Porosity Variability In Limestone Sequences  
 Reef Drilling  
 Sea Level Change and Its Effect on Reef Growth  
 Seismic Reflection  
 Solution Processes/Reef Erosion  
 Submarine Lithification

## OOIDS

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### Synonyms

Ooliths

### Definition

Ooids are spherical-sub spherical grains, consisting of one or more regular concentric lamellae around a nucleus, usually a carbonate particle or quartz grain.

Sediment composed of ooids is referred to as an *oolite*. The term ooid has been restricted to grains less than 2 mm in diameter and the term pisoid (formerly pisolith) is used for similar grains of a larger diameter. *Coated grain* is a general term frequently used for ooids and pisoids, and includes *oncoids*, grains with a microbial coating.

Ooids typically form in agitated shallow waters of sub-tropical seas where they are frequently moved as sand-waves, dunes and ripples by tidal and storm currents, and wave action. They are commonly found in association with reefs and reefal limestones; thus they often form along shelf-margins (e.g., the Bahamas), but they also occur in tidal-deltas and beach-barriers of shallow ramps (e.g., Trucial Coast, Arabian Gulf).

The majority of modern ooids range from 0.2 to 0.5 mm in diameter, are composed of aragonite and have a high surface polish. The characteristic microstructure is a tangential arrangement of acicular crystals, 2  $\mu\text{m}$  in length. Rarely ooids (and pisoids) form in quieter-water marine locations, such as lagoons and tidal flats, where a radial fabric is more common. Ooids can form in areas of strong wave action in lakes, where they usually have a dull, commonly, cerebroid (bumpy) surface. They may be composed of aragonite or calcite, or be bi-mineralic (low-Mg calcite–aragonite). These may be associated with stromatolite bioherms.

### Ancient marine ooids

Ooids in the rock record are generally composed of calcite (low Mg), but of these some were originally calcite (possibly high Mg), whereas others were originally aragonite. Primary calcite ooids, whether in high-energy or low-energy facies, typically have a radial texture of wedge-shaped, fibrous crystals, with an extinction cross under

crossed polars. Ancient ooids originally of aragonite will have been altered during diagenesis to a greater or lesser extent. Commonly, the aragonite has been dissolved out completely, to leave oomoulds, or these holes may be filled with calcite cement. Some ooids have a fine-grained micritic texture, mostly the result of micritisation by endolithic microbial organisms.

### Origin of ooids

Current ideas for the origin of ooids invoke inorganic or biochemical processes. For the former, the sea water in shallow tropical areas is supersaturated with respect to  $\text{CaCO}_3$ , so that this, together with water agitation,  $\text{CO}_2$  degassing and elevated temperature, is considered sufficient to bring about carbonate precipitation on nuclei. In a biochemical origin, the microbial processes in the organic mucilage (EPS) that coats and permeates the ooids create a microenvironment conducive to carbonate precipitation. The factors determining the primary mineralogy of ooids are water chemistry, especially  $P_{\text{CO}_2}$ , Mg/Ca ratio, carbonate saturation, and possibly the degree of water agitation. It is believed that aragonite and high-Mg calcite ooids are precipitated when  $P_{\text{CO}_2}$  is low and Mg/Ca ratio high, with opposite conditions for low-Mg calcite ooids. High carbonate supply, as would occur in high-energy locations, is thought to favour aragonite precipitation over high-Mg calcite.

There is a secular variation in the original mineralogy of ooids through the Phanerozoic, with aragonitic ooids, which may be associated with calcitic ooids (likely high-Mg calcite originally) in the late Precambrian/early Cambrian, mid-Carboniferous through Triassic and Tertiary to the Recent, and calcitic ooids (presumed to have low-to-moderate Mg content) dominant in the mid-Palaeozoic and the Jurassic–Cretaceous. This pattern, which correlates with the first-order, global sea-level curve, suggests a geotectonic mechanism(s) causing subtle variations in  $P_{\text{CO}_2}$  and/or Mg/Ca ratio in seawater. High sea-level stands, correlating with calcite seas, are times of high rates of sea-floor spreading, and high  $P_{\text{CO}_2}$  from increased metamorphism at subduction zones, and low Mg/Ca ratio from increased extraction of  $\text{Mg}^{2+}$  at mid-ocean ridges through seawater pumping.

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# P

## PACIFIC CORAL REEFS: AN INTRODUCTION

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### Introduction

This entry introduces coral reefs and associated archipelagos within or facing the Pacific Ocean, including those not sheltered behind adjacent western seas (Japan, Yellow, South China, Sulu, Celebes, Banda, Arafura); continents (Australia, Asia), and sub-continents (SE Asia, New Guinea). The Great Barrier Reef of Eastern Australia is within the Pacific Ocean but, like other regions, is covered in more detail in separate entries. A total of 47 archipelagos and isolated reefs and islands under the jurisdiction of 31 nations and territories in the Pacific are covered here and listed in [Table 1](#). The location and current names of most of the archipelagos and some of the nations are shown in [Figure 1](#). It is impossible to list and show all the governments and archipelagoes on one map or accurately estimate the number of tropical islands and reefs in the Pacific. However, there are likely more than 10,000 islands and associated reefs, far more than reported in [Table 1](#), which focuses mostly on the larger inhabited Pacific islands.

The Pacific supports the largest tropical and subtropical habitat for coral reefs in the world at about 58% of the global total, amounting to approximately 88 million km<sup>2</sup> between latitudes of 30° N to 30° S, based upon distance and area calculations of Google Earth imagery. This compares to about 35 million km<sup>2</sup> of habitat for the Indian Ocean, about 17 million km<sup>2</sup> of habitat for the Gulf of Mexico-Caribbean Sea, and 13 million km<sup>2</sup> of habitat for SE Asia. Along the Equator, the Pacific stretches from

127° E (off the eastern coast of Haimahera Island, north of New Guinea Island) to 80° W (off the western coast of Ecuador near Quito), a distance of 16,900 km and accounting for 42% of the circumference of the earth. Although the Pacific's huge size supports much larger numbers of coral reefs, tropical islands, large reefs, and habitat compared to those in the Indian Ocean and Gulf of Mexico-Caribbean Sea, the Pacific island number and size totals are less than those within SE Asia; much of the tropical and subtropical habitat in the Pacific is devoid of islands and reefs.

### Categories of reefs in the Pacific Ocean

All coral reefs begin as coral and/or coralline algal communities either along the sides and tops of emergent volcanoes near or above the sea surface within the Pacific Ocean basin or on preexisting substrates of the continents or continental islands bordering the Pacific. Periods of subsequent subsidence or uplift, tectonic plate movements, sea-level rises and falls, and other epochs of unfavorable ocean temperatures and chemistry during the Mesozoic and Cenozoic likely led to massive drowning, dissolution, and subduction of many ancient reefs. Not all of these were restored following the return of favorable conditions for their growth and survival. This chapter covers only living Pacific reefs comprising:

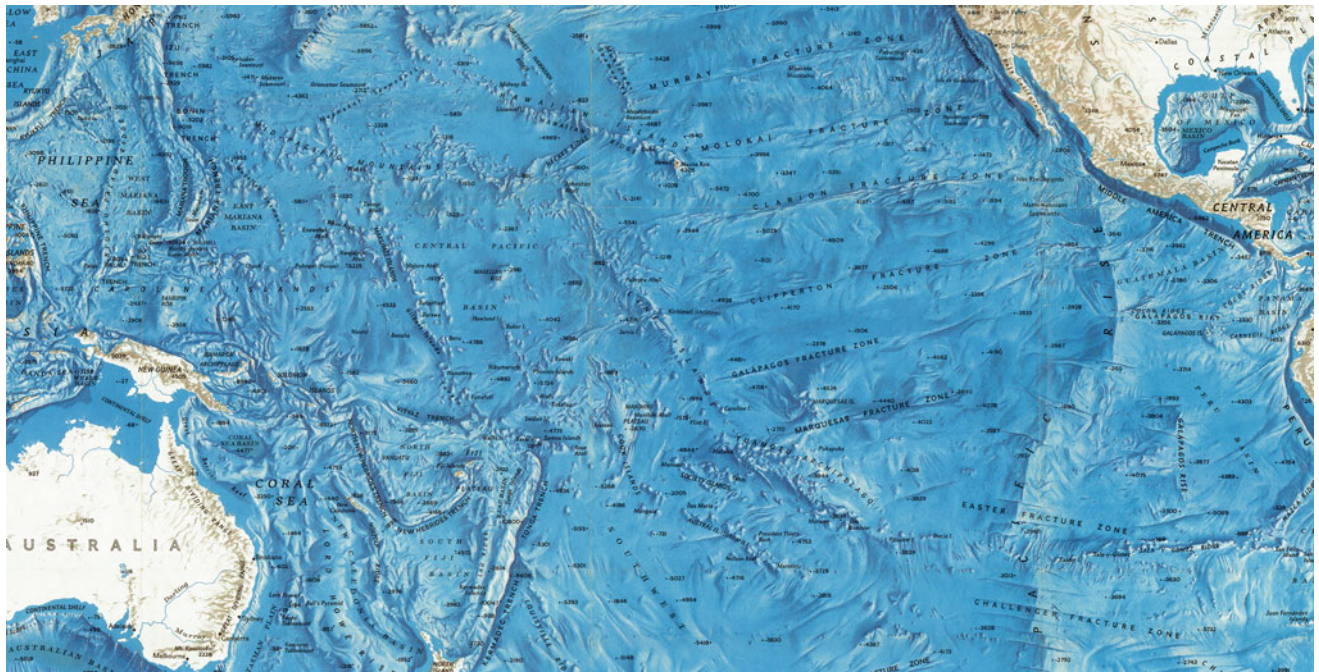
1. *Fringing reefs* – coral reefs that grow out and upwards to the sea surface directly from the shoreline of mostly volcanic or continental islands ([Figure 2](#)), starting out as aprons that may eventually encircle the fringes of islands and form shallow reef crests or flats.
2. *Barrier reefs* – linear offshore reefs that encircle subsiding or emerging volcanic islands offshore or on continental shelves beyond shallow lagoons that separate the barrier reefs from the island or continent ([Figure 3](#)).



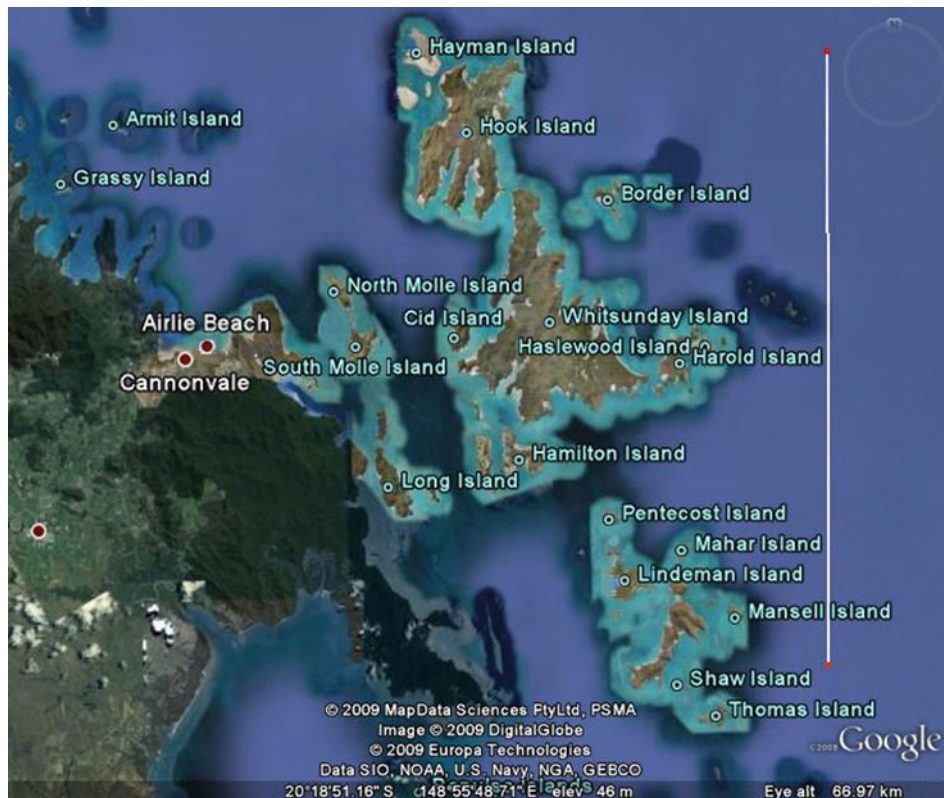
**Pacific Coral Reefs: An Introduction, Table 1** Comparing 47 coral reef archipelagos and single islands in the Pacific Ocean. Explanations: **bank** = submerged reef, **lag** = lagoon or marine lake, **areef** = atoll reef, **barr** = barrier reef, **low** = low reef island, **atol** = atoll, **lime** = raised limestone island or atoll, and closed atolls, **volc** = volcanic island with fringing reef, **all is** = total of all main islands, **tren** = tectonic trench nearby and likely contributing to island's formation, **cont** = continent or continental island, **bas** = basalt or oceanic island, **hot** = island or reef near to and likely formed over an oceanic hotspot, **1** (or more) = present, **0** = absent, and **nd** = no data. Area units = km<sup>2</sup>. Jurisdictions listed are at the highest independent national levels. Jurisdiction and archipelago names often differ, and archipelago names in brackets are those used during the twentieth century before political independence. Total number of islands and reefs are underestimated and focus on main inhabited islands, especially in the Solomon, Papua New Guinea, New Hebrides, Vanuatu, and Fiji Islands. (Sources: Bryan (1953), UNEP (1988), Dahl (1991), Maragos and Holthus (1998) National Geographic Society maps, Google Earth (2009), Reef Base, and Wikipedia web notes)

| Archipelago              | Jurisdiction     | Land – km <sup>2</sup> | Ocean – km <sup>2</sup> | Bank | Lag | Areef | Barr | Low | Atol | Lime | Volc | All is | Tren | Cont | Bas | Hot |
|--------------------------|------------------|------------------------|-------------------------|------|-----|-------|------|-----|------|------|------|--------|------|------|-----|-----|
| Admiralty – Bismarck     | Papua New Guinea | 462,841                | 3,120,000               | 0    | 22  | 0     | 1    | 24  | 26   | 9    | 18   | 60     | 1    | 1    | 0   | 0   |
| Austral                  | France           | 3,265                  | 5,030,000               | 12   | 3   | 0     | 2    | 12  | 1    | 2    | 14   | 31     | 0    | 0    | 1   | 1   |
| Caroline                 | FSM & Palau      | 1,193                  | 3,608,193               | 4    | 37  | 3     | 5    | 13  | 34   | 523  | 38   | 608    | 1    | 0    | 0   | 1   |
| Clipperton Is.           | France           | 9                      | 330,000                 | 0    | 0   | 0     | 0    | 0   | 0    | 1    | 0    | 1      | 1    | 0    | 1   | 0   |
| Cocos & Puerto Quepos    | Costa Rica       | 25                     | nd                      | 0    | 0   | 0     | 0    | 0   | 0    | 0    | 12   | 12     | 1    | 1    | 0   | 0   |
| Cooks                    | New Zealand      | 241                    | 1,830,000               | 1    | 3   | 0     | 2    | 2   | 7    | 4    | 6    | 19     | 0    | 0    | 1   | 1   |
| Coral Sea & Middleton    | Australia        | 354                    | nd                      | 2    | 1   | 8     | 0    | 5   | 4    | 1    | 2    | 12     | 0    | 1    | 0   | 0   |
| D'Entrecasteaux.         | Papua New Guinea | 3,100                  | see PNG                 | 0    | 1   | 50    | 1    | 1   | 7    | 0    | 5    | 13     | 1    | 1    | 0   | 0   |
| Fiji – Lau               | Fiji             | 18,274                 | 1,290,000               | 0    | 22  | 33    | 22   | 15  | 9    | 10   | 810  | 844    | 1    | 1    | 0   | 0   |
| Galapagos                | Ecuador          | 7,880                  | 45,000                  | 0    | 0   | 0     | 0    | 0   | 0    | 0    | 125  | 125    | 1    | 1    | 1   | 0   |
| Gambiers                 | France           | 31                     | see Austral             | 0    | 1   | 2     | 0    | 0   | 1    | 0    | 13   | 14     | 0    | 0    | 1   | 1   |
| Guadalupe – Socorro      | Mexico           | 406                    | nd                      | 0    | 0   | 0     | 0    | 0   | 0    | 1    | 20   | 21     | 1    | 1    | 1   | 1   |
| Gilbert                  | Kiribati         | 810                    | 3,550,000               | 0    | 12  | 0     | 0    | 6   | 10   | 2    | 0    | 18     | 0    | 0    | 1   | 0   |
| Ha'apai Group            | Tonga            | see Tonga              | nd                      | 2    | 4   | 0     | 2    | 6   | 0    | 15   | 41   | 62     | 1    | 1    | 0   | 0   |
| Hawaii                   | United States    | 16,629                 | 2,147,985               | 32   | 10  | 1     | 2    | 1   | 5    | 2    | 24   | 32     | 0    | 0    | 1   | 1   |
| Indonesia – West Pacific | Indonesia        | nd                     | nd                      | 0    | 7   | 0     | nd   | 9   | 7    | 0    | nd   | 16     | 1    | 1    | 0   | 0   |
| Kermadecs                | New Zealand      | 33                     | nd                      | 0    | 0   | 0     | 0    | 0   | 0    | 0    | 15   | 15     | 1    | 1    | 0   | 0   |
| Lines                    | Kiribati & US    | 515                    | nd                      | 2    | 6   | 1     | 0    | 4   | 5    | 2    | 0    | 11     | 0    | 0    | 1   | 0   |
| Louisiades               | Papua New Guinea | 1,790                  | 26,000                  | 0    | 18  | 0     | 12   | 60  | 17   | 2    | 21   | 100    | 1    | 1    | 0   | 0   |
| Marianas                 | United States    | 1018                   | 2,041,000               | 1    | 3   | 0     | 2    | 2   | 0    | 5    | 12   | 19     | 1    | 1    | 1   | 0   |

|                        |                    |           |            |    |     |     |    |     |     |     |      |       |    |    |    |    |
|------------------------|--------------------|-----------|------------|----|-----|-----|----|-----|-----|-----|------|-------|----|----|----|----|
| Marquesas              | France             | 1,049     | 0          | 0  | 0   | 0   | 0  | 0   | 1   | 0   | 0    | 16    | 17 | 0  | 1  | 1  |
| Marshall Islands       | Marshall Is. & US  | 181       | 0          | 30 | 0   | 0   | 0  | 5   | 30  | 0   | 0    | 0     | 35 | 0  | 1  | 0  |
| Minami Torishimas      | Japan              | 1.2       | 0          | 0  | 0   | 0   | 0  | 0   | 1   | 0   | 0    | 0     | 1  | 0  | 1  | 0  |
| Nauru                  | Nauru              | 21        | 0          | 1  | 0   | 0   | 0  | 0   | 0   | 1   | 0    | 0     | 1  | 0  | 1  | 0  |
| New Caledonia          | France             | 19,060    | 4          | 14 | 38  | 4   | 16 | 19  | 4   | 1   | 1    | 5     | 44 | 1  | 1  | 0  |
| Niue I                 | New Zealand        | 259       | 0          | 0  | 0   | 0   | 0  | 0   | 0   | 1   | 0    | 0     | 1  | 0  | 1  | 1  |
| Ogasawara (Bonin)      | Japan              | 73        | 0          | 0  | 1   | 0   | 1  | 0   | 1   | 0   | 1    | 30    | 32 | 1  | 1  | 0  |
| Perlas & Chiriqui      | Panama             | 394       | 0          | 0  | 0   | 0   | 0  | 0   | 0   | 0   | 0    | 47    | 47 | 1  | 1  | 0  |
| Phoenix Is             | Kiribati – US      | 31.4      | 2          | 3  | 0   | 0   | 7  | 3   | 0   | 0   | 0    | 0     | 10 | 0  | 1  | 0  |
| Pitcairn & Henderson   | United Kingdom     | 43        | 0          | 2  | 0   | 0   | 1  | 1   | 1   | 1   | 4    | 0     | 0  | 1  | 1  | 0  |
| Rapa Nui               | Chile              | 166       | 0          | 0  | 0   | 0   | 0  | 0   | 0   | 0   | 1    | 1     | 1  | 0  | 1  | 1  |
| Sala y Gomez           | Chile              | 0.15      | 0          | 0  | 0   | 0   | 0  | 0   | 0   | 0   | 2    | 0     | 2  | 0  | 1  | 1  |
| Ryukyus                | Japan              | nd        | 0          | 0  | 0   | 0   | 0  | 0   | 0   | 0   | 61   | 61    | 1  | 1  | 0  | 0  |
| Samoa                  | Samoa & US         | 3240      | 10         | 3  | 0   | 0   | 1  | 1   | 1   | 1   | 16   | 19    | 1  | 0  | 1  | 1  |
| Society                | France             | 1,680     | 0          | 13 | 0   | 8   | 8  | 5   | 1   | 9   | 23   | 0     | 0  | 1  | 1  | 1  |
| Solomon                | Solomon Is.        | 28,450    | 1          | 13 | 9   | 19  | 16 | 19  | 8   | 955 | 998  | 1     | 1  | 0  | 0  | 0  |
| Solomon Sea            | Papua New Guinea   | see PNG   | 1          | 6  | 0   | 1   | 3  | 6   | 4   | 2   | 15   | 1     | 1  | 0  | 0  | 0  |
| South China Sea        | Peoples Rep. China | nd        | nd         | nd | 1   | nd  | 22 | 3   | nd  | nd  | 25   | 0     | 1  | 0  | 0  | 0  |
| Taiwan                 | Republic of China  | 35,980    | 0          | 0  | 0   | 0   | 0  | 0   | 0   | 0   | 6    | 0     | 2  | 0  | 0  | 0  |
| Tokelaus               | NZ & US            | 11        | 0          | 3  | 0   | 0   | 1  | 3   | 0   | 0   | 0    | 0     | 4  | 0  | 1  | 0  |
| Tongatapu Group        | Tonga              | 718       | 0          | 3  | 0   | 0   | 13 | 0   | 53  | 5   | 71   | 1     | 1  | 1  | 0  | 0  |
| Torres Strait          | Australia & PNG    | nd        | nd         | 2  | 0   | 0   | 3  | 2   | 0   | nd  | 274  | 1     | 1  | 0  | 0  | 0  |
| Tuamotu                | France             | 885       | 0          | 72 | 0   | 1   | 5  | 71  | 1   | 1   | 78   | 0     | 0  | 1  | 0  | 0  |
| Tuvalu (Ellice)        | Tuvalu             | 26        | 1          | 6  | 0   | 0   | 3  | 6   | 0   | 1   | 9    | 0     | 0  | 1  | 1  | 0  |
| Vava'u Group           | Tonga              | see Tonga | 0          | 0  | 0   | 0   | 2  | 0   | 15  | 24  | 41   | 1     | 1  | 0  | 0  | 0  |
| Vanuatu (New Hebrides) | Vanuatu            | 12,190    | 0          | 1  | 1   | 0   | 15 | 1   | 38  | 34  | 88   | 1     | 1  | 0  | 0  | 0  |
| Wallis & Futuna        | France             | 278       | 0          | 1  | 0   | 1   | 0  | 0   | 0   | 3   | 3    | 1     | 0  | 1  | 1  | 1  |
| Totals                 | 47                 | 625,451   | 35,299,966 | 75 | 323 | 148 | 85 | 284 | 303 | 708 | 2394 | 3,943 | 25 | 24 | 26 | 14 |



**Pacific Coral Reefs: An Introduction, Figure 1** Mercator projection map of the marine geology and named archipelagos, trenches, and fracture zones in the Pacific Ocean Basin between Latitudes 30° N and 30° S (Source of map: National Geographic Society).



**Pacific Coral Reefs: An Introduction, Figure 2** Fringing reefs encircling the Whitsunday Islands (20° 19'S, Latitude and 145° 56'E, Longitude) inside the Central Great Barrier Reef off north east Australia (Source Map Data Sciences Pty. Ltd. PSMA Image (2009) : Digital Globe (2009), Europa Technologies (2009) and Google Earth (2009).



3. *Submerged reefs* – living reefs on the tops of subsided volcanoes that are within water depths of 0–30 m, that may cause waves to break upon them, but that do not support emergent reefs or islands (Figure 4).
4. *Atoll reefs* – similar to the above except the reefs reach near the sea surface and encircle a protected lagoon without supporting emergent vegetated islands (Figure 5).
5. *Atolls* – similar to the above except that the atoll supports one or more vegetated islets and its reefs partially or wholly encircle a lagoon and allow regular surface interchange of waters between the ocean and lagoon (Figure 6).
6. *Low reef islands* – Similar to atolls in that they grow upwards off the crests of subsiding volcanoes, reach the sea surface, and support one or more emergent vegetated reef islets, but lack the size or shape to support a perimeter reef encircling a lagoon (Figure 7).
7. *Raised limestone islands and atolls* – similar to atolls and reef islets except that living reefs are limited to the submerged perimeter fringes facing the ocean. The interior parts are raised above sea level to elevations where reef builders (such as corals, coralline algae) cannot survive due to constant aerial exposure, causing the emergent part of the reef to weather and erode, often to limestone, and often creating inland marine lakes that lack regular surface water exchange with the ocean (Figure 8).
8. *Closed atolls* – similar to raised atolls except that they are near sea level but with interior marine lakes completely land-locked by the islands and blocking all surface seawater exchange with the ocean (Figure 9).
5. *Southern subtropical Pacific* – consisting of small volcanic and reef islands north of New Zealand and east of Australia, including the Kermadec, Elizabeth, Middleton, Norfolk, and Lord Howe islands and reefs.
6. *Southwestern continental border* – consisting of the continental shelf islands and reefs from the southern end of the Great Barrier Reef to the Torres Strait.
7. *Southwestern tropical Pacific* – dominated by many large and small volcanic continental islands, numerous raised reef islands, and approximately 100 atolls and reef islets in Papua New Guinea, Solomon Islands, Vanuatu, Fiji, Tonga, Samoa, and New Caledonia.
8. *Northwestern tropical Pacific* – consisting of two dozen volcanic islands, several hundred raised reef islands, and about 100 atolls and reef islets including the Marshall Islands, Mariana Islands, Gilbert [Tungaru] Islands of Kiribati including Nauru and Banaba, Caroline Islands (Palau and Federated States of Micronesia), and a few offshore reefs and atolls east of the southern Philippines and Indonesia.
9. *Northwestern subtropical continental border* – including the Ogasawara [Bonin], Ryukyu, and Minami Torishima [Marcus] islands of Japan; Taiwan; and other small islands and reefs in open South China Sea north of the Philippines.

The archipelagos and isolated islands in the Pacific can be grouped into about nine clusters based upon biogeography, geology, and cultural history (Figure 10). Beginning at due north and moving clockwise, these consist of:

1. *Subtropical Hawaiian Islands* – consisting of Hawaii and Johnston Atoll, including two dozen small to large volcanic basalt islands, several atolls, and two low reef islands.
2. *Eastern tropical continental border* – consisting of one closed atoll (Clipperton) and several volcanic island clusters off the continental shelves and slopes of the Americas from Mexico through Costa Rica and Panama to Ecuador and including the Galapagos.
3. *Southeast tropical insular Pacific* – consisting of scattered basalt volcanic islands, a hundred atolls and reef islets, and one raised limestone island (Makatea), and one raised atoll (Henderson) collectively within French Polynesia, Pitcairn, Rapa Nui, and Sala y Gomez.
4. *Central tropical Pacific* – consisting of about 50 atolls and reef islets and a few raised limestone and small basalt volcanic islands south of Hawaii and north of Samoa, and including the Phoenix, Line, Cook, Tokelau, Ellice [Tuvalu] archipelagos, Niue Island, and Rose Atoll.

## Geology

Most of the contemporary Pacific Ocean is bounded by a “Ring of Fire” (Figure 11a), with dozens of volcanoes, deep ocean trenches, and mountain ranges lining the border that separates the oceanic (basalt) crust of the central Pacific Ocean basin from adjacent continental crust of islands and continents. About 200 million years ago, the Pacific Ocean was part of a single ancient global ocean before tectonic activity during the Permian began to fragment it along with the single continent (Pangaea) into smaller continental and ocean plates that have continued to collide and/or drift apart to this time. Eventually this led to segregation of the Pacific from the Indian Ocean and dissecting and fragmenting continental and oceanic crusts between the two emerging oceans to create what is now SE Asia.

Over the past 100 million years, the massive Pacific Ocean plate has continued to produce and move new crust in a northwestern direction via convection flow beneath the East Pacific Rise and collisions with the adjoining Nazca Plate off the west coast of South America. The Pacific plate is continuing to move slowly towards the trenches of NE Asia, Siberia, and the Aleutians where eventually it is subducted under them. Additionally, the Asian continental plate is encroaching on the Pacific Ocean Plate from the NW, the Australian continental plate is encroaching from the west, and the two American continental and Nazca plates from the east, creating massive continental mountain ranges and trenches bordering the Pacific plate. These movements and collisions generate earthquakes, landslides, volcanism, tsunamis, uplift, and



**Pacific Coral Reefs: An Introduction, Figure 3** Taha'a Island and surrounding barrier reef (June 2000 image; 16° 38' S Latitude and 151° 30' W Longitude) and 10 km scale bar, Society Islands, French Polynesia (Source: Europe Technologies Image (2009), DigitalGlobe (2009), and Google Earth (2009)).

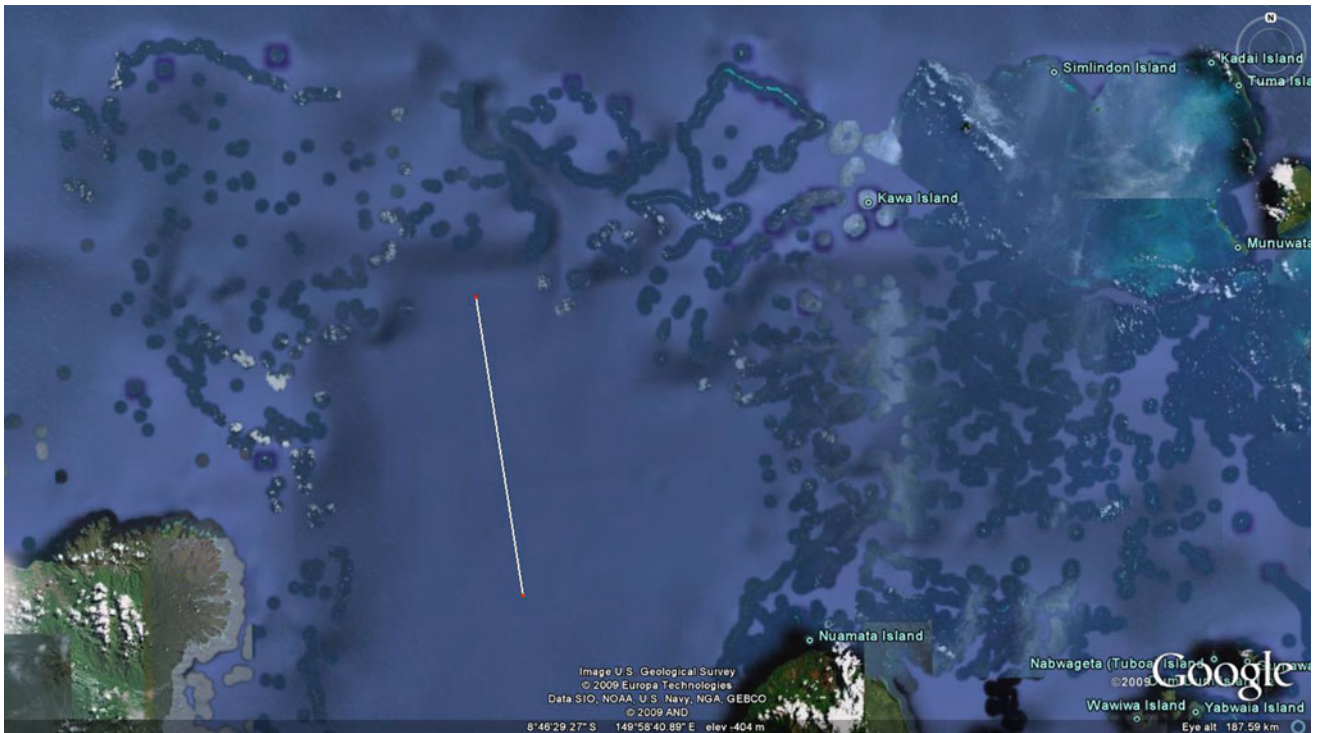
other seismic events. As the broad Pacific plate creeps towards the NW, parts of it move at different rates and directions, creating fracture zones, volcanic hotspots, earthquakes, subsidence, emergence, and flexures that have further contributed to the rise and fall of dozens of volcanic archipelagos at hotspots on the plate over the past 80–100 million years (Figures 11a and b). Overall, central Pacific archipelagos are now generally older towards the NW and younger towards the SE margins of the plate. Conversely, larger and more numerous islands are concentrated in the SW tropical Pacific but are virtually absent in the tropical and subtropical East Pacific. Deep ocean trenches separate the continents from the Pacific Ocean around most of the latter's perimeter. Moreover, much of the southwestern Pacific region is bisected by several trenches stretching from the western end Samoa through Tonga, Vanuatu, Solomons, etc. (see Schellart et al., 2006).

#### **Oceanographic and climatic processes affecting Pacific coral reefs**

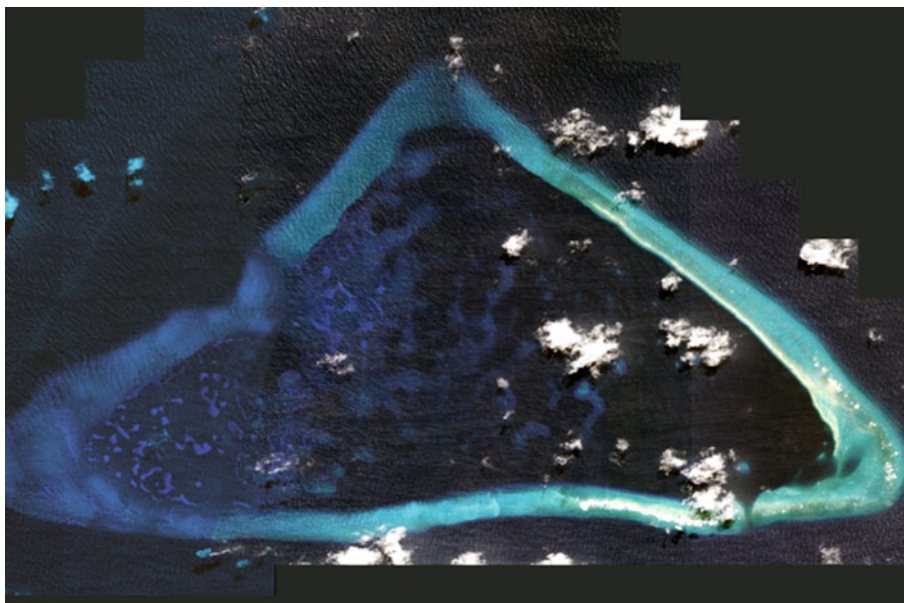
A system of circular surface ocean currents, called gyres, dominates circulation in the Pacific and other large oceans

(Figure 12). The gyres move clockwise in the northern hemisphere and counterclockwise in the southern hemisphere, and greatly influence the diversity of reef life and distribution of Pacific reefs. In the northern hemisphere, the cold California Current runs south along the west coast of North America from Alaska to southern Mexico and then turns west where it is named the North Equatorial Current. As this current runs west along the broader Pacific in low latitudes, it heats up before turning north, named the Kuroshio Current that runs along the east coast of Japan and Siberia, bathing the reefs at higher latitudes with warmer waters. Then the current turns east off Siberia where it is named the Subarctic Current that cools off as it travels east at high latitudes towards Alaska before it turns south as the California Current again, continuing its circular clockwise movement in the northern Pacific.

The gyre in the southern hemisphere is a mirror image of the northern gyre. The cold Peru Current runs north along the west coast of South America, and turns west off Ecuador where it is named the South Equatorial Current that heats up along its long journey across the South Pacific at low latitudes. Some of this current moves west through the Torres Strait, but most runs through



**Pacific Coral Reefs: An Introduction, Figure 4** Large complex of submerged reefs with 50 km scale bar ( $8^{\circ} 46' S$  Latitude and  $149^{\circ} 59' E$  Longitude), off the Western D'Entrecasteaux Islands, Papua New Guinea (Source: U.S. Geological Survey (2009), Europa Technologies (2009), and Google Earth (2009)).



**Pacific Coral Reefs: An Introduction, Figure 5** Example of atoll reef at Kingman Reef National Wildlife Refuge, Line Islands ( $6^{\circ} 24' N$  Latitude and  $162^{\circ} 24' W$  Longitude). Length of reef is 15 km (Source of image: NASA and Lead Dog Consulting).





**Pacific Coral Reefs: An Introduction, Figure 6** Example of an atoll at Hereheretue Atoll, October 2006 ( $20^{\circ} 53' S$  Latitude and  $144^{\circ} 58' W$  Longitude) with a 3 km scale bar, Tuamotu Islands, French Polynesia (Source of image: Europa Technologies (2009), DigitalGlobe (2009), and Google Earth (2009)).



**Pacific Coral Reefs: An Introduction, Figure 7** Example of a low reef islet at Flint Island, March 2009 ( $11^{\circ} 26' S$  Latitude and  $151^{\circ} 49' W$  Longitude), with a 5 km scale bar at the southern end of the Line Islands (Source of image: DigitalGlobe (2009), Lead Dog Consulting (2009), Geoeye (2009), and Google Earth (2009)).



**Pacific Coral Reefs: An Introduction, Figure 8** Example of a raised limestone island at Banaba [Ocean] Island, April 2005 (00° 52' S Latitude and 169° 32' E Longitude), west of the Gilbert Islands and with a 3 km scale bar (Source: DigitalGlobe (2009) and Google Earth (2009)).

the large islands of the SW Pacific before turning south off NE Australia and is known as the East Australia current that helps to extend corals and reefs as far south as Brisbane. Then at high latitudes, the current turns east to join the broad, cold West Wind Drift that encircles the globe north of Antarctica. A branch of the West Wind Drift moves towards South America and turns north off Chile and is known as the Peru Current again, continuing the gyre's circular counterclockwise cycle.

The forces that drive these currents are heat exchange between low and high latitudes, the NE trade-winds in the northern tropics, the SE trade-winds in the southern tropics, and the rotating Earth's Coriolis Effect (describing mathematically the deflection of moving formations and masses, i.e., winds, ocean currents, clouds, aircraft, etc., caused by their inertia relative to the earth, a non-inertial uniformly rotating frame of reference). Trade-winds at the sea surface act to drag and mix the surface waters, pushing up sea level on the western ocean boundary to a slightly higher elevation vis-à-vis the eastern ocean boundary of the Pacific. The movement of both the NE and SE trade-wind systems towards low latitudes eventually causes them to collide and then rise skyward along an atmospheric band at about 5° N Latitude. These air masses then cool off and drop large amounts of rain in

a zone where surface winds are weak. This band of wet calm surface waters is the Inter-tropical Convergence Zone (ITCZ). The ITCZ weakens, strengthens, and shifts north and south depending on the strength of the trade-winds and the seasons.

Because the surface trade-wind drag is weak or absent beneath the ITCZ, a return flow of ocean water moving "down-slope" from the elevated western Pacific to the lower eastern Pacific is maintained as the North Equatorial Countercurrent. There is also a smaller South Equatorial Countercurrent at approximately 8° S Latitude and a sub-surface Equatorial Undercurrent that also runs west to east at the Equator. The eastward flow of water in these currents transports the larvae of many reef species from the biodiversity-rich western Pacific to the central and eastern Pacific. The warm water currents along the western boundary of the Pacific help to extend the range of many reef species to higher latitudes. Conversely, the cooler waters off the eastern boundary of the Pacific off the Americas may be another reason why reef development is generally poor in the East Pacific. All of the above current and wind systems are essential for exchanging heat between cooler polar areas and warmer tropical areas of the ocean and maintaining steady and predictable temperature regimes for corals and other reef life. Conversely,



**Pacific Coral Reefs: An Introduction, Figure 9** Example of a closed atoll, Clipperton Island ( $10^{\circ} 18' \text{ N}$  Latitude and  $109^{\circ} 13' \text{ W}$  Longitude) and its marine lake SW of Mexico. Clipperton is one of the most northeastern reefs in the Pacific Ocean (Source: Europa Technologies (2009), DigitalGlobe (2009), NASA (2009), and Google Earth (2009)).

when the wind systems break down during El Nino Southern Oscillations (ENSO) at low latitudes, water temperatures rise, causing corals to bleach and/or die, and slowing down the flow of currents vital for survival of many migratory marine organisms including fish and sea-birds (see entry “*Climate Change and Coral Reefs*”).

Tropical cyclones are also concentrated along specific “alleys” in the western and eastern central Pacific, and their effects are sufficient to limit the three-dimensionality, growth, and biodiversity of many reefs, especially in the Philippine, Taiwan, Mariana, Caroline, Papua New Guinea, Solomon, Samoa, and Cook archipelagos, and lesser so in most other Pacific archipelagos.

### Geography and biogeography of the tropical Pacific Ocean

The oceanic, climatic, and geological history of the Pacific Ocean has led to the contemporary distributional patterns of its islands, reefs, and dominant reef life as showed by Figures 11a and b:

1. Mostly, atolls and reef islands dominate the central Pacific along an axis from the Pitcairn and Tuamotu Islands at the SE and Marshall Islands and Marcus Island at the NW end of the axis (Figure 13). This region of the ocean is geologically stable, allowing

ancient volcanic islands to subside and allow formation of atolls, a dozen barrier reefs, and reef islands in accordance with Darwin’s theory.

2. Numerous volcanic islands of continental origin are to the west and south of oceanic basalt islands to the north and east. Many of the SW Pacific islands are large, representing the consequence of considerable tectonic activity over long time periods (Figure 1).
3. Numerous raised limestone islands along the west Pacific boundary and isolated volcanic islands with limestone caps in the central Pacific populate the Pacific Ocean. This is likely the result of collisions between the Pacific, Asian, and SE Asian plates, causing the Pacific crust to buckle and push coral reefs above sea level, creating volcanic island arcs above the subduction zones (Figure 14).
4. Smaller high-volcanic island chains and seamounts are scattered haphazardly over the tropical Pacific crust near a combination of hotspots, fracture zones, and flexures that allow volcanism to penetrate upwards through to Pacific crust to form islands that may later subside and serve as the substrates for a variety of coral reefs (Figures 11a and b).

At a Pacific-wide scale are vast expanses of the tropical Pacific that lack islands and coral reefs, particularly the eastern Pacific (Figures 11a and b), while the SW Pacific





**Pacific Coral Reefs: An Introduction, Figure 10** The location of the Eastern Pacific Barrier and the nine clusters of island archipelagos and coral reefs in the Pacific Ocean as explained in the text. (1) Subtropical Hawaiian Islands, (2) Eastern Continental Tropical Border, (3) Southeast Tropical Insular Pacific, (4) Central Tropical Pacific, (5) Southern Subtropical Pacific, (6) Southwest Tropical Continental Border, (7) Southwest Tropical Pacific, (8) Northwest Tropical Pacific, and (9) Northwest Subtropical Continental Border.

archipelagos have exceptionally high densities and larger coral reef habitats. The large timeframe and spatial distance of separation of East Pacific reefs from the rest of the reefs in the Central and Western Pacific has led to differentiation in evolution of species of corals and perhaps other reef-dwelling organisms. The broad zone between the two subregions lacking islands and reefs is referred to as the East Pacific Barrier. Additionally, there are still substantial distances between many of the archipelagos in the central and western Pacific, and their separate histories have also led to lesser levels of differentiation of their biological and geological characteristics and biodiversity. Most conspicuous is that the richness of coral reef and related marine species increases when moving from east to west across the Pacific. This increasing trend towards the western Pacific applies to all coral reef and related shallow-water tropical biota for which sufficient data are available, including: reef building corals, reef fishes (Figure 15), other reef invertebrates, algae, sea grasses, and mangroves.

Ongoing research, including that of Coral Geographic scientists are now compiling patterns for coral species richness at the archipelagic scale and have further proposed a “coral triangle” area where coral diversity reaches its highest global levels, including SE Asia and the SW Pacific areas of the Solomons and Papua New Guinea. The pattern of increasing species that totals towards the west is generally maintained at the archipelagic level throughout the Pacific (Figures 16). However, recent

research and analyses by the present authors covering more than 2,200 site surveys at 70 reefs of various types in the Central Pacific reveal that there is significant small-scale heterogeneity between reefs based upon the coral species richness and the complement of coral species reported at each (Figures 17 and 18). Among these reefs were found 25 significantly different clusters, including substantial differences in species compositions and richness between adjacent reefs. Although data analyses had not been completed, the principal factors explaining these clusters appear to be:

- Latitudinal proximity to the North Equatorial Countercurrent
- Longitude (distance from the “coral triangle”)
- Size of each reef or island
- Proximity to the nearest reef
- Size of the nearest reef, and
- Type of reef

These factors may help explain how especially geographic isolation, reef size, proximity to other reefs, and boundary currents can contribute substantially to our understanding of the biogeography of corals and their patterns of biodiversity, dispersal, and endemism throughout the tropical Pacific. However, these same factors may have different effects or be less influential for other reef biota, especially fishes that have greater mobility during both their adult and larval stages, and to algae that produce spores that remain viable over long time periods and distances. In



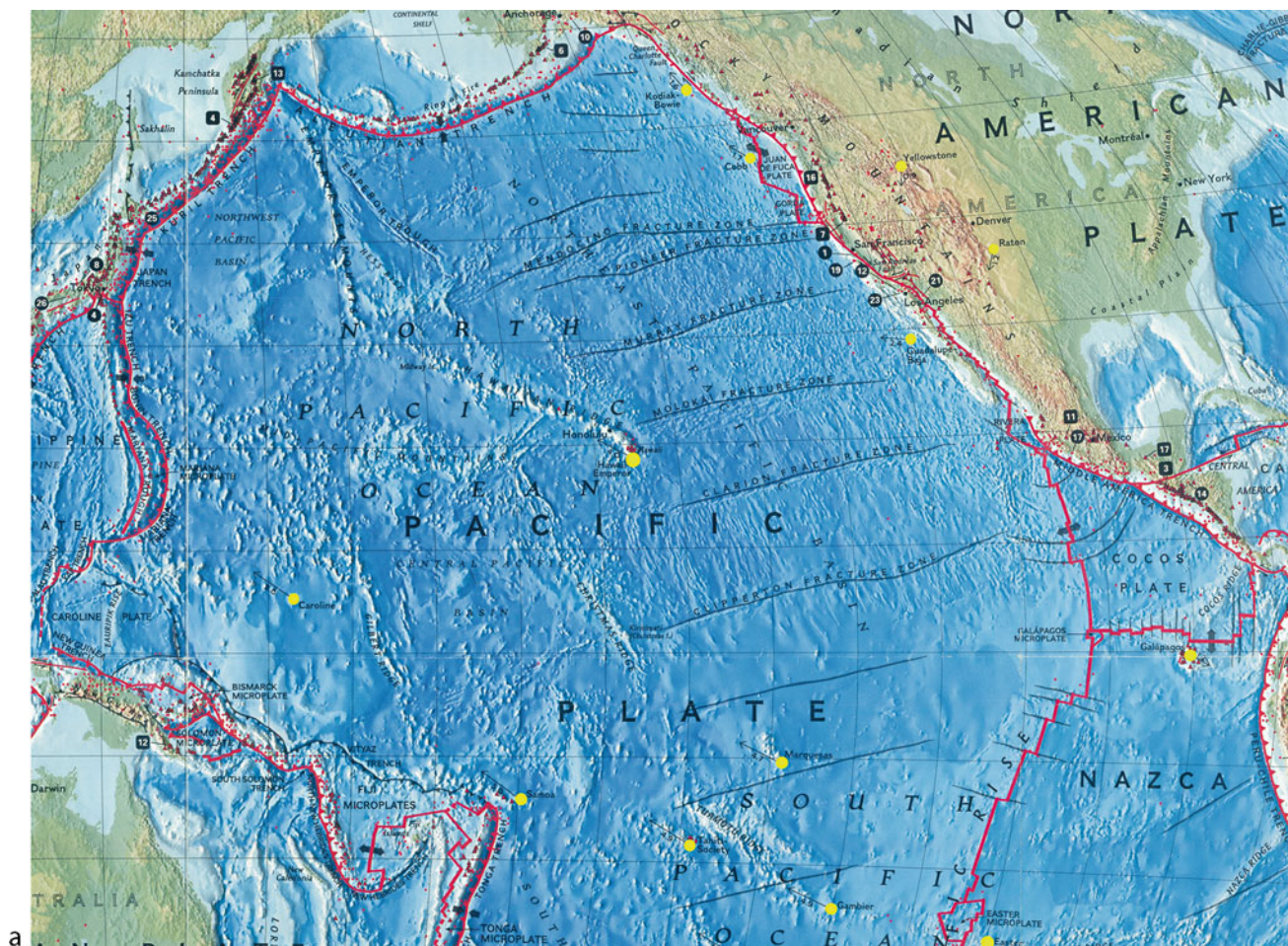
the past, theories of radiation and accumulation have been put forth to explain the broader scale biodiversity levels in the western Pacific, but these are insufficient for explaining patterns at smaller spatial scales (Maragos and Williams, in preparation). Certainly there is mounting evidence that the “coral triangle” region has contributed many of the species in the Pacific, but it is also clear that localized endemism and speciation at isolated reefs have also contributed additional species within the distant and isolated corners of the Pacific Ocean.

### Early cultural settlement of the central Pacific Ocean

Linguistics, oral history, legends, field archaeology, radio-carbon dating, artifacts (fish hooks, pottery, etc.), pollen

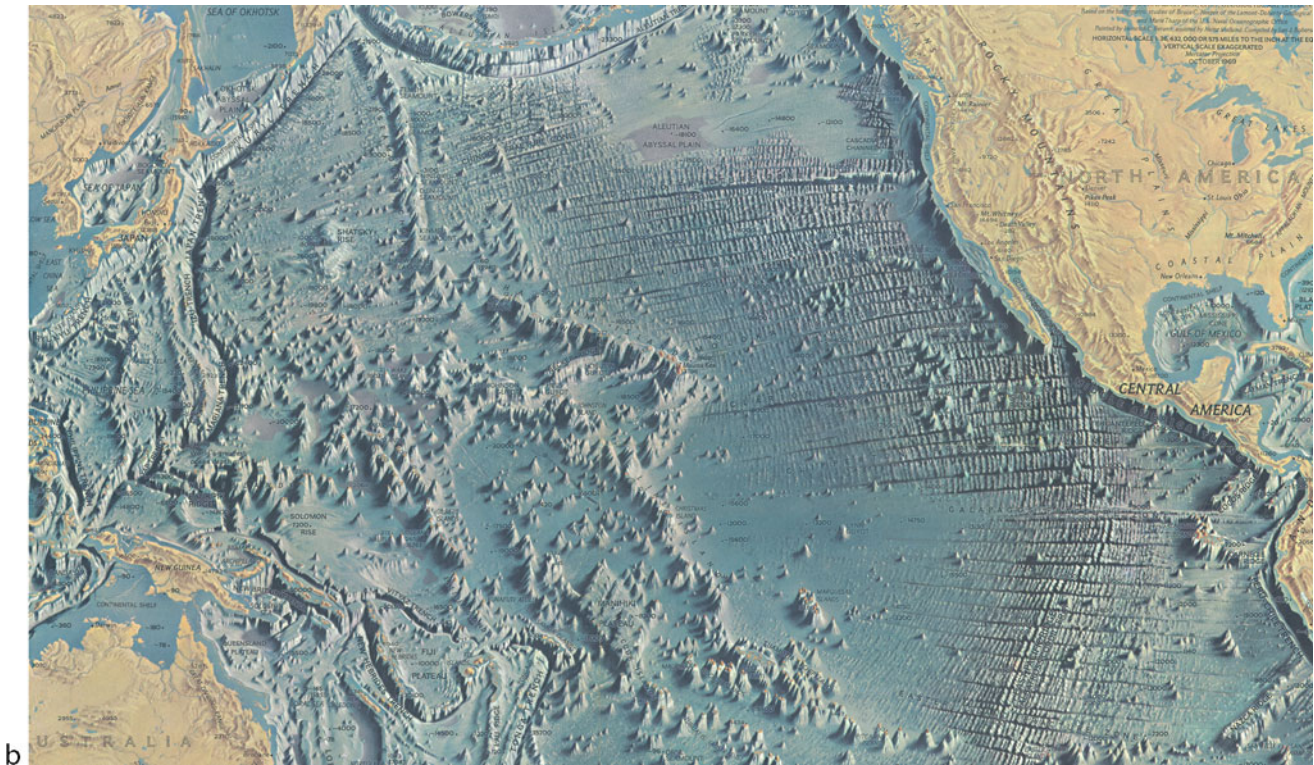
analyses, and molecular analyses suggest that there are three broad cultural groups that settled within the insular tropical Pacific, also known as Oceania, after the last glacial recession about 10,000 year ago. These are still the principal cultures resident in most of the islands of Oceania today (Figure 19):

- *Melanesia*. Settlers first reached the SW Pacific Islands of Fiji, New Caledonia, Papua New Guinea, Solomon Islands, Vanuatu more than 10,000 years ago from Southeast Asia and the Indian Ocean regions (Bellwood 1978; Rainbird 1994).
- *Micronesia*. Settlers from the Philippines first reached the NW Pacific islands about 5,000 years ago beginning with the Mariana Islands and then to the Caroline,



**Pacific Coral Reefs: An Introduction, Figure 11** (a) Broad map of the Pacific Ocean plate tectonics showing the “Ring of Fire” (red lines) where the Pacific Plate is colliding with several continental plates, and about ten hot spots (yellow circles). A hot spot is a superheated stationary spot deep in the earth’s mantle resulting in upward movement of volcanic magma and penetration through the oceanic crust of the Pacific Plate and causing submarine volcanic eruptions and formation of island archipelagoes, in the Pacific Crust that have spawned volcanic archipelagos. The East Pacific Rise is at the SE corner of the Pacific where the Pacific and Nazca Plates collide, and about ten named longitudinal fracture zones are to the northwest. (Source of map: National Geographic Society). (b) Marine geological floor of the Pacific Ocean showing vertically exaggerated island groups, seamounts, fracture zones, trenches, and the East Pacific Rise along the SE boundary of the Pacific Plate with the Nazca Plate (Source of map: National Geographic Society).





Pacific Coral Reefs: An Introduction, Figure 11 (Continued)

Marshall, and Gilbert (Tungaru) archipelagos and the two raised islands of Banaba (Ocean Islands) and Nauru, near the Gilberts.

- **Polynesia.** The migrants departed from what is now the Maluku Province of Indonesia about 5,000 years ago and eventually settling in the Pacific about 3,000 years ago at Tonga and Samoa and then slowly moving eastward to what is now the Society Islands in the SE Central Pacific. Then between 1,100 and 600 years ago, a second, broader series of migrations occurred in several waves, beginning with Tahitians and later generations of evolving Polynesian cultural groups who moved:
  1. Westward to what are now known as the Cook, Niue, Tokelau, Tuvalu, New Zealand Islands
  2. Northward to the Marquesas and Hawaiian Islands
  3. Eastward to what are now known as the Tuamotu, Pitcairn, and Easter [Rapa Nui] Islands
  4. Southward to the Austral and Gambier Islands, and then
  5. Northwestward towards the Carolines, Fiji, northern Solomon Islands, and northern Papua New Guinea, including islands previously settled by Melanesians and Micronesians.

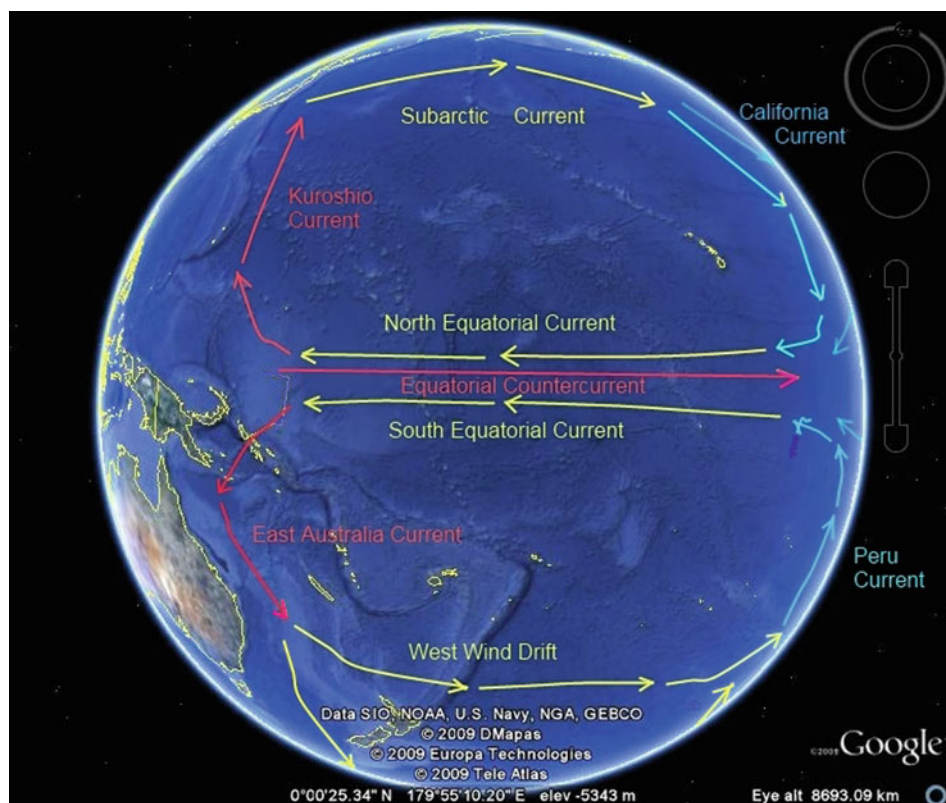
Samoans also reached the previously settled Gilbert and Tokelau Islands within the last 800 years. It is also likely

that Polynesians reached South America before the era of European rediscovery (Figure 20). Several island groups (Phoenix, Line) in the central Equatorial Pacific were visited by both Polynesians and Micronesians but were not permanently settled at the time of first European explorers 500 years ago, although some were later settled during the past century of European colonial rule.

### Political history of the Pacific since the European rediscovery

Spanish explorers were the first Europeans to discover and navigate across the Pacific Ocean in the early sixteenth century. Spain was also the first to establish colonies at Guam and several Northern Mariana Islands. Other Spanish, French, and British explorers during the sixteenth to eighteenth centuries were mostly exploring, seeking, or transporting gold, silver, pearls, spices, jewels, silks, and trepang. The French, British, and Americans eventually established colonies and/or developed plantation agriculture, forestry, ranching, or mining on some of the larger islands by the mid-nineteenth century (Fiji, New Caledonia, New Hebrides [Vanuatu], Tahiti, New Zealand, Australia, Hawaii). In 1876, Germany began establishing large colonies in the Pacific including Nauru, Papua New Guinea, Western Samoa, Northern Mariana, Caroline, and Marshall Islands. In turn, this prompted other





**Pacific Coral Reefs: An Introduction, Figure 12** Global projection of the Pacific Ocean showing the major surface currents in the northern and southern hemispheres. Red – warm western ocean currents, blue – cold eastern ocean currents, and yellow – cross-ocean currents at intermediate temperatures that are either warming up or cooling off (Source of base map: D Mapas (2009), Europa Technologies (2009), Tele Atlas (2009), and Google Earth (2009)).

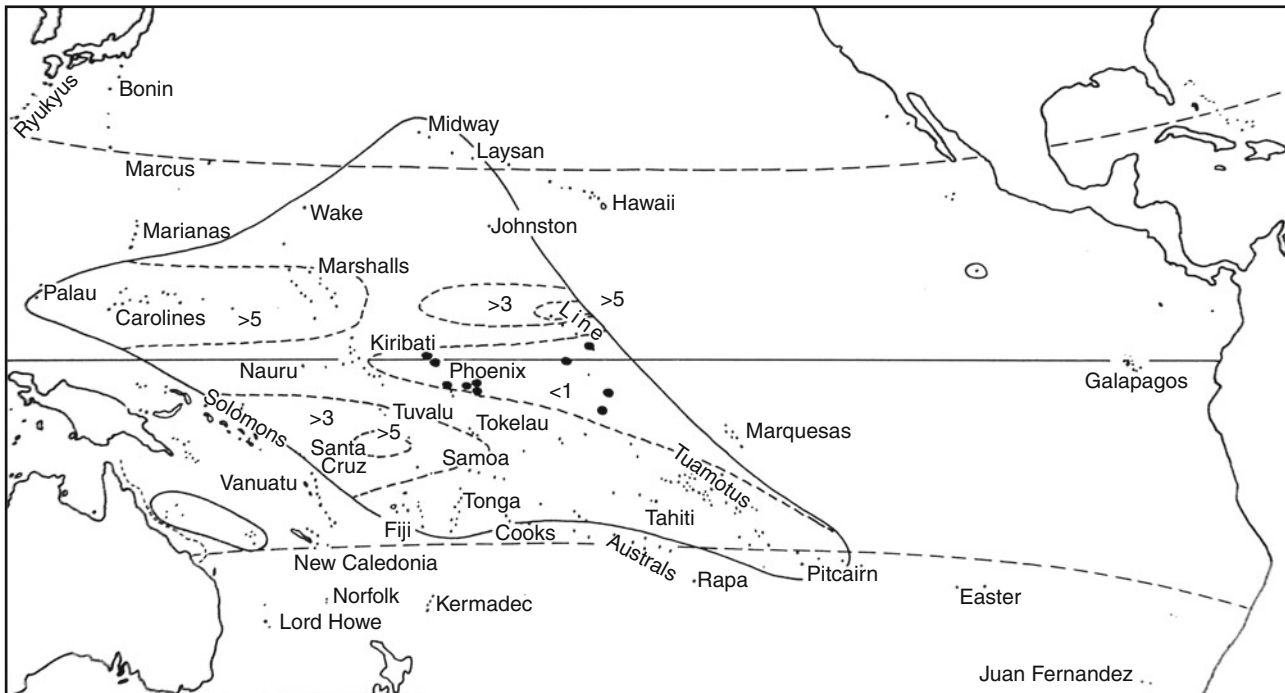
world powers to annex islands or establish colonies in the rest of the strategically important Pacific. Of special importance was mining of guano because of its agricultural value as a fertilizer and ingredient for gunpowder. France and Great Britain established territories in French Polynesia, Wallis and Futuna, New Hebrides [Vanuatu], Solomon Islands, Gilbert Islands, and Ellice [Tuvalu] Islands. The US annexed the Philippines, Hawaii, American Samoa, Guam, Wake Atoll, Midway Atoll, and the Panama Canal Zone between 1898 and 1903, and the US and Great Britain also claimed smaller islands previously mined for guano.

After Germany declared war at the outbreak of World War I (WWI) in Europe in 1914, Japan seized German colonies in the Marshall, Caroline, and Mariana Islands while New Zealand, Australia, and Great Britain took custody of the remaining German possessions after WWI and the defeat of Germany. After 1935, Japan began fortifying its Pacific possessions, and the USA, Great Britain, and Australia claimed and/or fortified additional islands in the Line, Tuvalu [Ellice], Solomon, Gilbert, and Phoenix Islands and Papua New Guinea. After WWII and creation of the United Nations, a dozen inhabited trust territories were designated (Figure 20) with the goal of preparing them

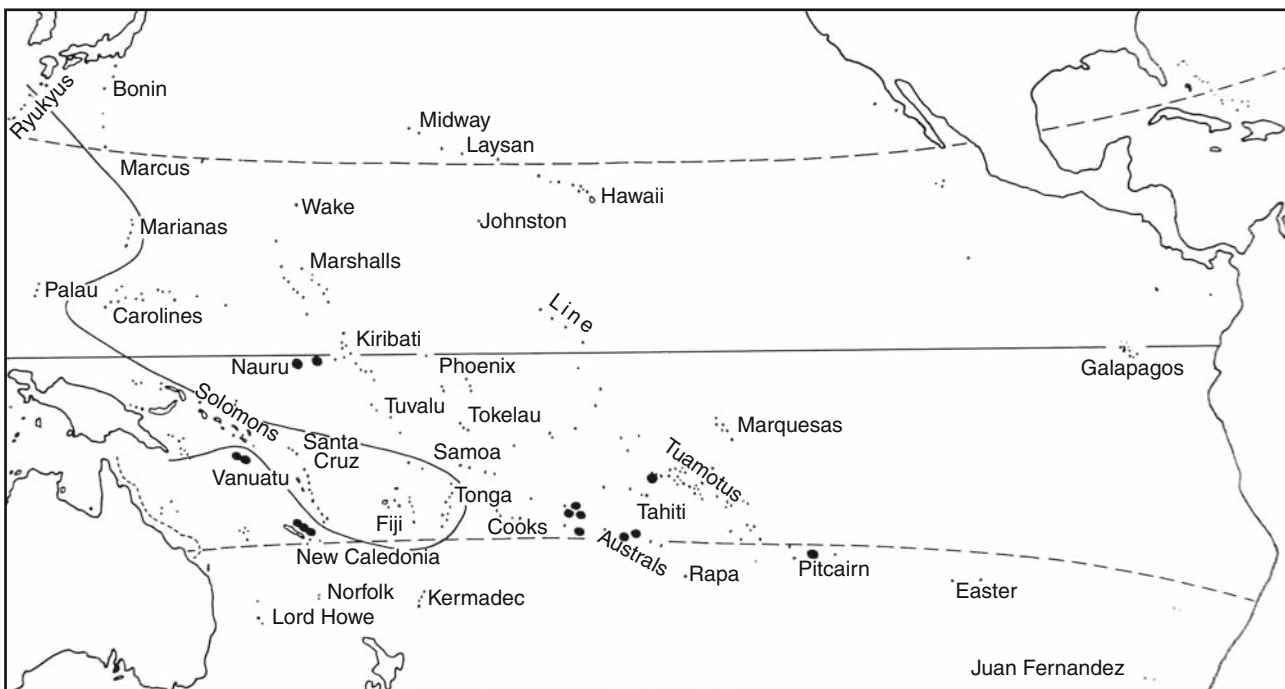
for self rule and democracy; these primarily included inhabited islands claimed, captured, and colonized before and between the two world wars. Most of the Pacific islands are now independent republics or democratically governed territories and protectorates as voted upon and chosen by the resident populations (see Table 1). Only the Kingdom of Tonga has been spared the colonialism experienced by all other Pacific cultures during the past five centuries. The economies of the islands have now shifted to fisheries, tourism, agriculture, ranching, mariculture, mining, and military defense. The emerging island nations also continue to respect their traditional cultures and control of lands and marine areas for subsistence and conservation to maintain valued resources, including coral reefs.

### Status of and threats to Pacific coral reefs

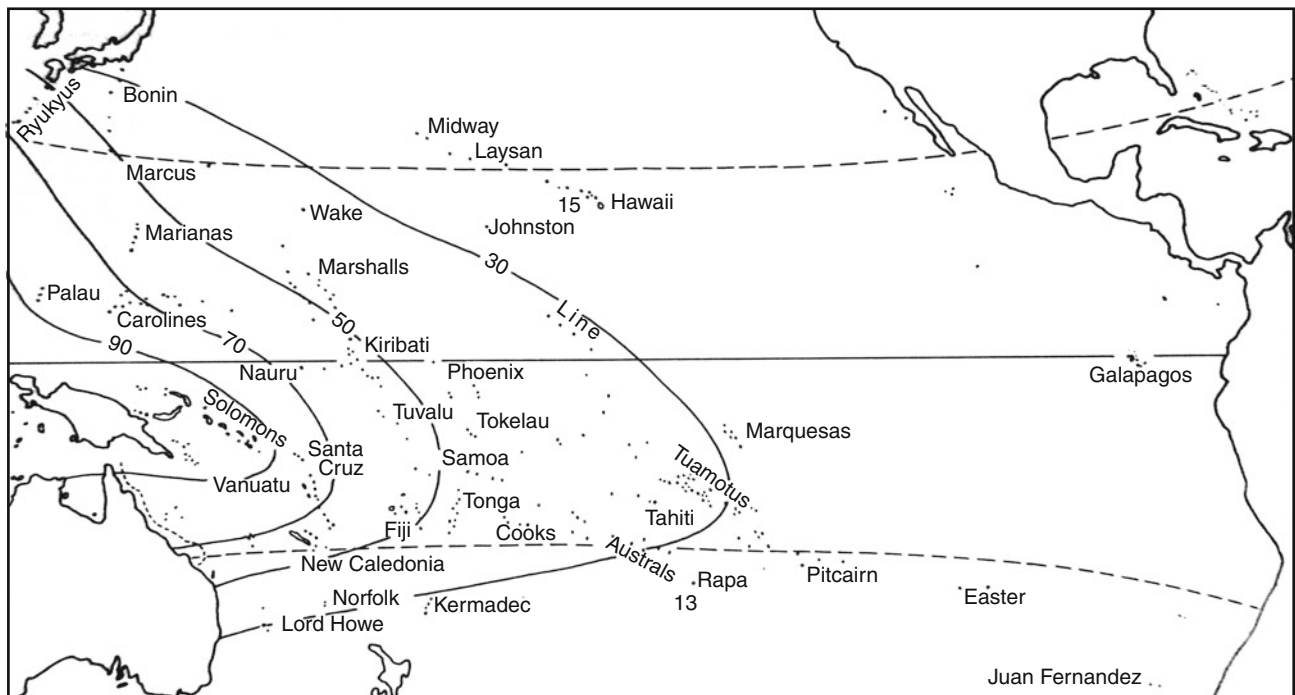
The massive size of the Pacific Ocean combined with low human population densities and high buffering capacity has to date spared most of its coral reefs from the degradation experienced by reefs in the other oceans and seas where human populations are much denser. The largest marine-protected areas (MPAS) in the world are now established in the Pacific including the Great Barrier Reef



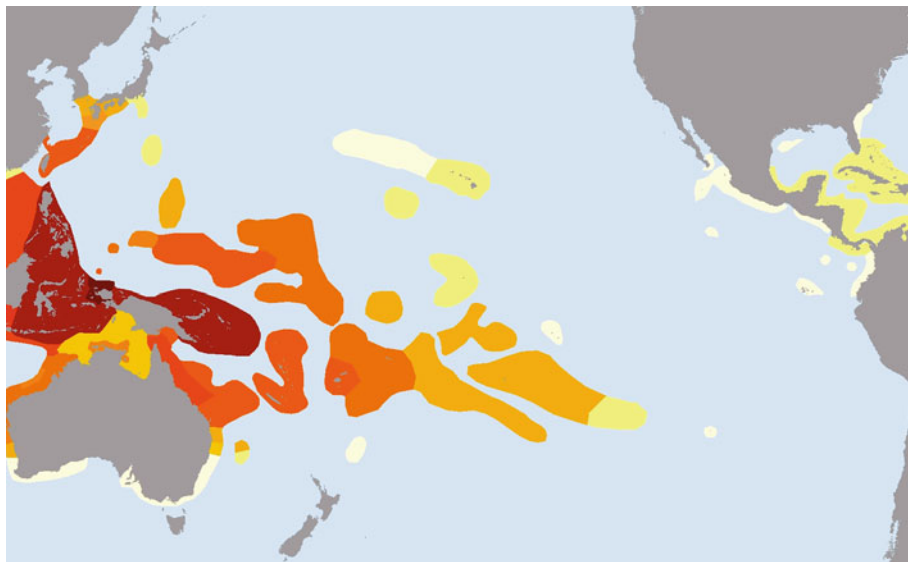
**Pacific Coral Reefs: An Introduction, Figure 13** Distribution of low reef islands and atolls and about a dozen raised limestone islands in the central Pacific (Source: Stoddart (1992)).



**Pacific Coral Reefs: An Introduction, Figure 14** Distribution of high limestone islands primarily along in the western Pacific, with many to the west of the solid line. Black circles are Makatea Islands or volcanic islands with substantial Makatea limestone (Source: Stoddart (1992)).

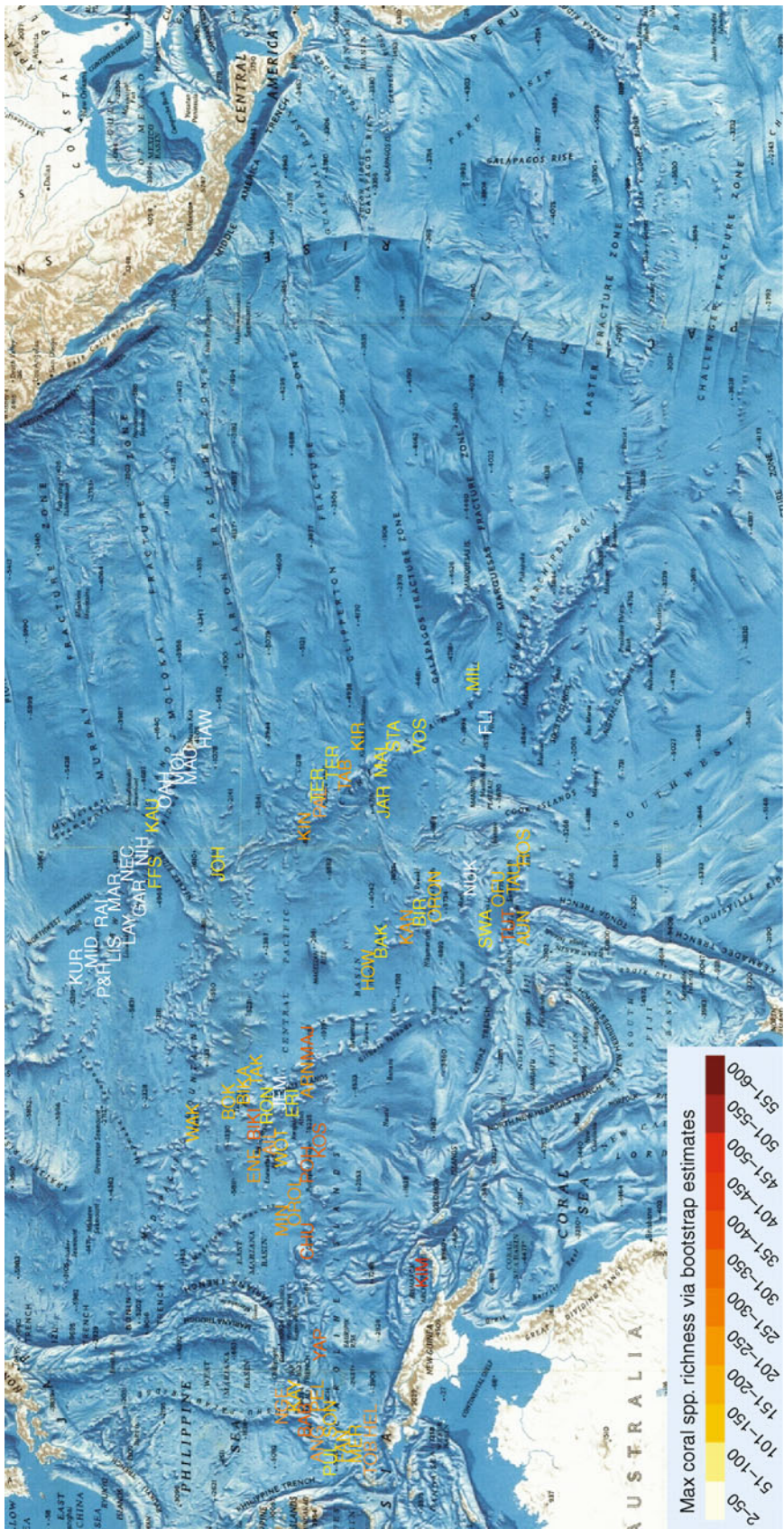


**Pacific Coral Reefs: An Introduction, Figure 15** Lines of increasing families of warm water fishes towards the western Pacific Ocean (Source of data: Springer (1982) in Stoddart (1992)).

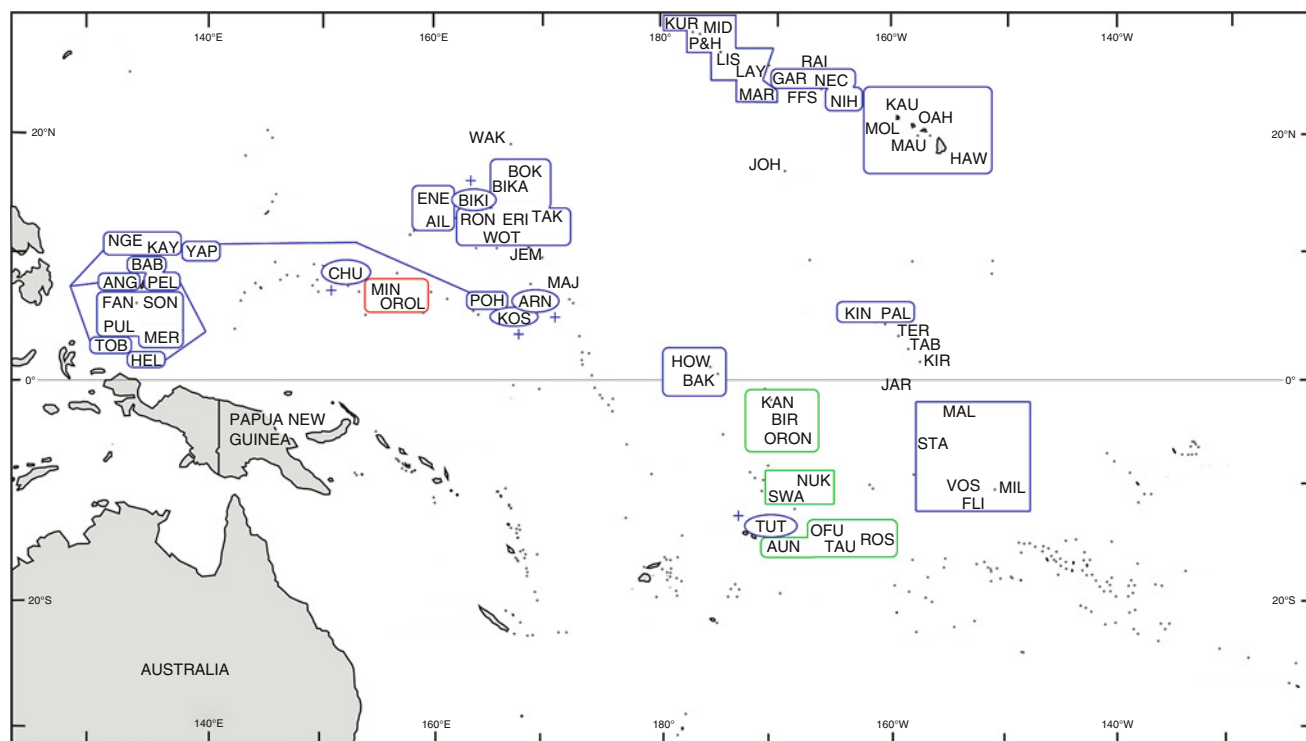


**Pacific Coral Reefs: An Introduction, Figure 16** Coral species richness at Pacific archipelagos showing increasing trends towards the western Pacific and the Coral Triangle. Color legend shows white for lower levels of diversity through increasing shades of yellow, orange, and red for higher levels of diversity. Map after Coral Geographic, J.E.N Veron et al. (2009).





**Pacific Coral Reefs: An Introduction, Figure 17** Color-based coral species richness levels at 70 individual islands and reefs in the Pacific. Color legend follows the same scale as in Figure 16, with white lowest and red highest in species richness per island or reef. Reef codes (in parentheses): A = atoll, B = barrier reef, C = closed atoll, I = volcanic island, L = raised limestone island, R = reef, and S = submerged reef. Explanations for island names, in alphabetical order for both Figures 17 and 18: AIL = Ailinginae (A), ANG = Angaur (I), ARN = Arno (I), AUN = Aunu'u (I), BAB = Babeldaob (B), BAK = Baker (I), BIK = Bikini (A), BIR = Birnie (I), BOK = Bokaak (A), CHU = Chuuk (B), ENE = Enewetak (A), ERI = Erikub (A), FAN = Fanna (I), FFS = French Frigate Shoals (A), FLI = Flint (I), Gardiner Pinnacles (I), Hawai'i (I), HEL = Helen Reef (A), HOW = Howland (I), JAR = Jarvis (I), JEM = Jemo (I), JOH = Johnston (A), KAN = Kanton (A), KAU = Kaua'i (I), KIM = Kimbe Bay (B), KIN = Kingman Reef (R), KIR = Kiritimati (A), KOS = Kosrae (I), KUR = Kure (A), LIS = Lisianski-Neve (A), MAJ = Majuro (A), MAL = Malden (L), MAR = Maro (R), MAU = Maui (I), MER = Merir (I), MID = Midway (A), MIL = Millennium (A), MIN = Minto (R), MOL = Moloka'i (I), NEC = Necker (I), NGE = Ngeruagil-Velasco (R&S), NIH = Nihoa (I), NUK = Nukunonu (A), OAH = O'ahu (I), OFU = Ofu-Olosega Islands (I), OROL = Oroluk (A), ORON = Orona (A), P&H = Pearl and Hermes (A), PAL = Palmyra (A), PEL = Peliliu (I), POH = Pohnpei (B), PUL = Pulo Anna (I), RAIT = Raita Bank (S), RON = Rongerik (A), ROS = Rose (A), SON = Sonsorol (I), STA = Starbuck (L), SWA = Swains (C), TAB = Tabueraan (A), TAK = Taka (A), Ta'u (I), TER = Teraina (I), TOB = Tobi (I), TUT = Tutu'ila (I), VOS = Vostok (L), WAK = Wake (A), WOT = Wotia (A), and YAP = Yap (B). (Source: Maragos and Williams (in preparation)).



**Pacific Coral Reefs: An Introduction, Figure 18** Results of multivariate similarity profile analyses comparing the coral species compositions among the same 70 islands and reefs of Figure 17. Results show 25 statistically distinct clusters among the 70 reefs (green = < 60%, blue = 60–80%, red = > 80% similarity). Locations left unmarked form a “cluster” in isolation (e.g., JOH.). Lines connect spatially separated locations that form an individual cluster (e.g., POH and YAP). Five locations that are extremely spatially separated form an individual cluster, indicated by “+”. Preliminary multivariate analyses indicate that longitude, proximity to the North Equatorial Countercurrent, size of reef, distance to nearest reef, and size of neighboring reefs all may be important contributing factors. Island codes listed in caption for Figure 20 (Source: Maragos and Williams (in preparation)).

of Australia, Northwestern Hawaiian Islands, several northern Line Islands, Phoenix Islands, much of New Caledonia’s reefs, and marine areas around the Mariana Trench. Several more of the northern Marshall Islands and the southern Line Islands may also be formally protected soon as MPAS, and there are hundreds of smaller MPAS now scattered throughout the Pacific.

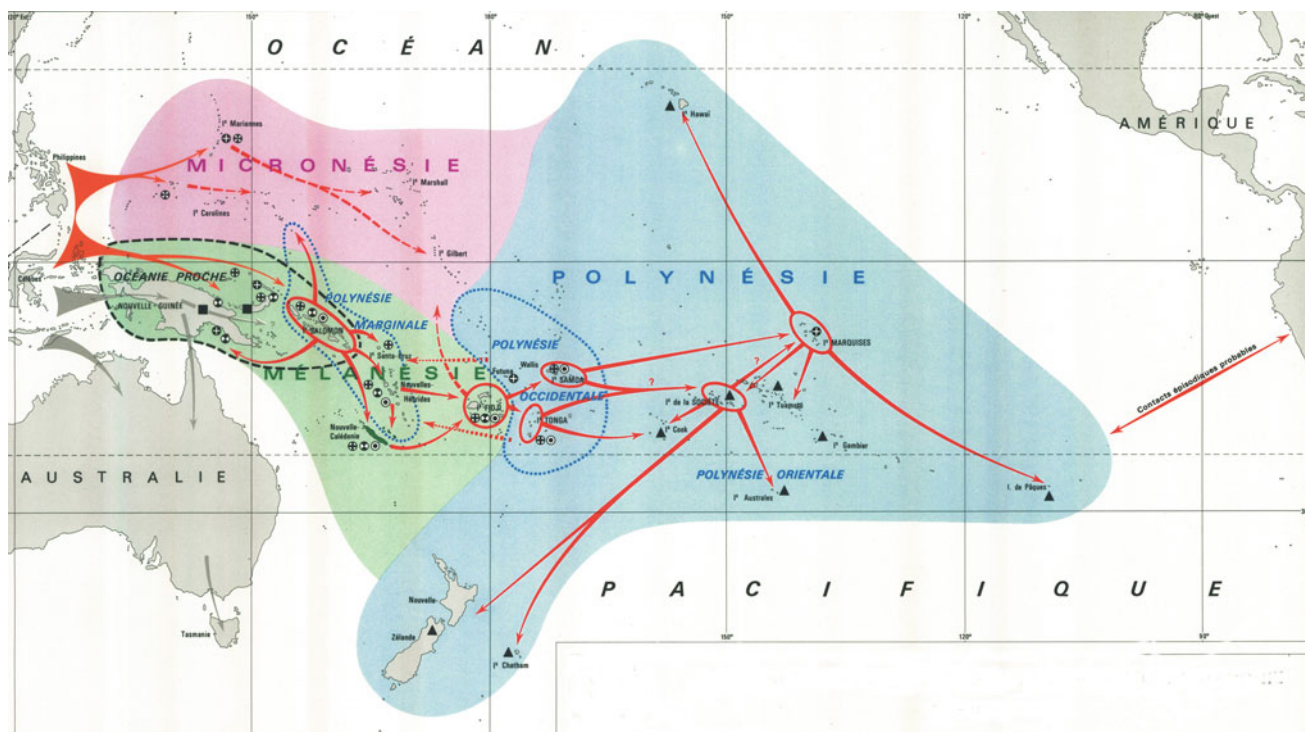
The major existing impacts to Pacific reefs are sea surface temperature anomalies, tropical cyclones, tsunamis, urban pollution, coastal construction, and over-fishing near population centers, exacerbating coral disease, bleaching and excessive predation by crown-of-thorn sea stars (*Acanthaster*), and localized dominance of invasive species. Additionally there are residual effects of WWII construction of military bases and related battles, and the postwar impacts of the USA, British, and French nuclear testing programs in the Pacific.

### The future of Pacific coral reefs

Despite the generally excellent status of many of its reefs at this time (Riegl and Dodge 2008), Pacific coral reefs

and related islands face an uncertain future. Past development proposals that would have adversely affected Pacific reefs may arise again: a sea-level canal through Central America; use of atolls and islands for garbage disposal, storage of nuclear waste, commercial missile-launching sites, oil transshipment facilities, and desalinization plants. The unauthorized poaching of fish and use of destructive fishing methods is already a major concern, especially near uninhabited islands and reefs where fish stocks are plentiful. Also, incidents of grounded and wrecked fishing vessels on remote reefs are on the rise. Emerging Asian economies and demand for fish are depleting tuna and other commercial fishing stocks in other oceans and East Asian seas, and compelling Pacific nations to enter into unenforceable fishery treaties that support foreign plans to establish fish processing bases throughout the tropical Pacific. During the past two centuries, wooden sailing vessels with poor navigation capabilities avoided remote reefs and islands for fear of crews being wrecked, grounded, stranded, or eaten by sharks. Now, thousands of modern steel-hulled fishing vessels with GPS are plying the Pacific in search of islands, reefs,





**Pacific Coral Reefs: An Introduction, Figure 19** Map showing the migration and settlement patterns of the Pacific islanders throughout Oceania over the past several millennia (Source of map: ORSTOM 1981).

sharks, and other fishing grounds, often far from the watchful eyes of residents and the limited enforcement assets of their governments.

### Responses to global climate change

Sea level, tropical cyclone, and temperature rises and possibly ocean acidification pose as serious threats to reefs worldwide (see entry “*Climate Change and Coral Reefs*”). However, many remote Pacific reefs may harbor greater resilience to these impacts due to the lack of present-day direct anthropogenic impacts. Although sea-level rise may destroy islands and force islanders off low islands and atolls, the reefs themselves may continue to survive and grow upwards. However, endemic and indigenous wildlife (nesting seabirds and sea turtles, resting shorebirds, Hawaiian monk seals) on low uninhabited and undisturbed atolls and reef islands will be most at risk as their island habitats are washed away. Emergency habitat development and translocations may be needed for many species to save them. Many of these islands now have alien rats and cats that prey on smaller ground-nesting seabirds, especially petrels, shearwaters, and terns.

Many undisturbed Pacific reefs would serve as excellent field laboratories to assess the effects of global climate change not complicated by other anthropogenic effects. Appendix A is a listing and catalogue of intact reefs

(1) at the margins in the Pacific, and (2) along the Equator that could serve as excellent field laboratories for climate-change research, spanning the spectrum of Pacific climatic and oceanic habitats.

### Summary and conclusions

The Pacific Ocean is the World’s last true frontier on Earth. We are still in the discovery and inventory phase as to understanding the wealth and diversity of coral reefs and the reef life that inhabits or depends upon them. Pacific reefs remain in excellent condition at this time, although Asian economic expansion and global climate change are now beginning to threaten these coral reefs and their inhabitants. Islanders that dwell on low reef islands and atolls will likely need to be evacuated, while many terrestrial wildlife species on low uninhabited islands may need to be saved from extinction. The nations and cultures within Oceania should consider forming their own federation to protect and care for islanders who will need assistance and new homes, and save island wildlife species threatened with extinction. Some of the key elements of such a federation would be to:

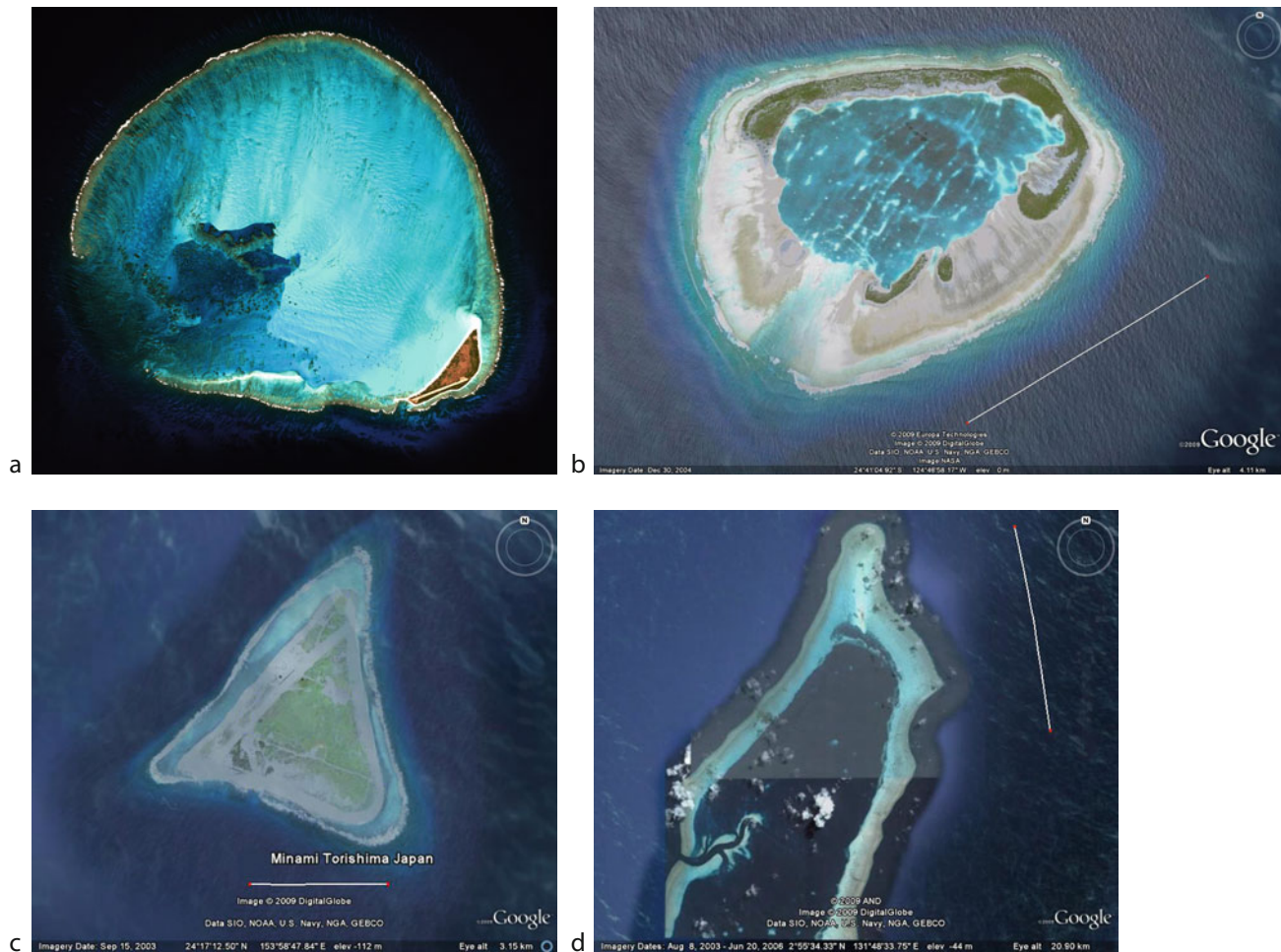
- Promote ecological and climate-change research to better respond to the future
- Research and develop remote surveillance technology to discourage unauthorized fishing and access





Pacific Coral Reefs: An Introduction, Figure 20 Map showing post-WWII Pacific Ocean archipelagos, governments, and Trust Territories. Water current patterns are also shown (Source of map: National Geographic Society).





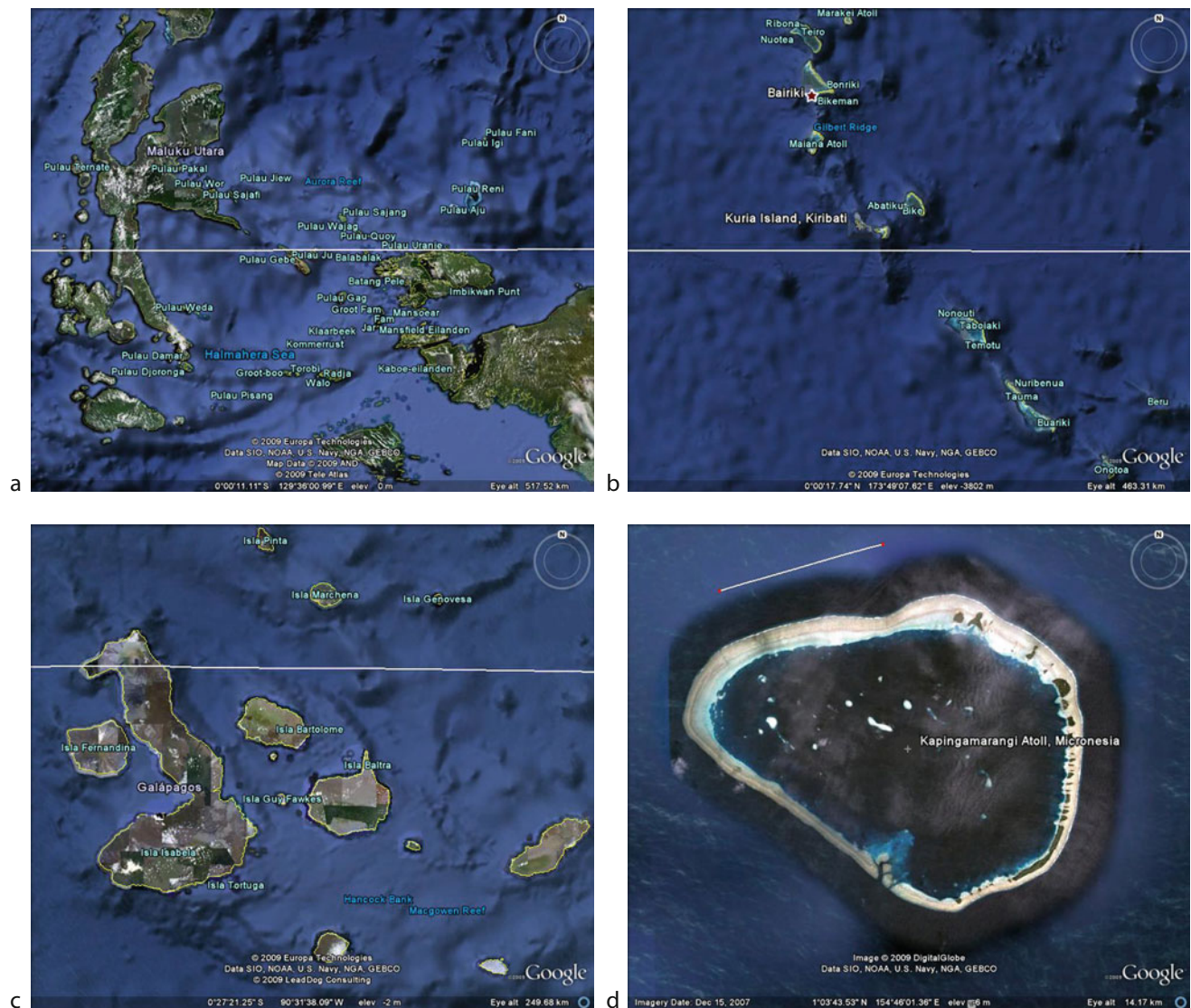
**Pacific Coral Reefs: An Introduction, Figure 21** (a) Kure Atoll (2004 image) at the northern tip of the Northwestern Hawaiian Islands, and the northernmost atoll in the Pacific Ocean ( $28^{\circ} 25' N$  Latitude and  $178^{\circ} 20' W$  Longitude). Maximum diameter of atoll is 7 km. Image processed by D. Siciliano. (Source of image: Quickbird Imagery and DigitalGlobe (2009)). (b) Aerial image of Ducie Atoll (December 2004), the most southeastern atoll in the subtropical Pacific ( $24^{\circ} 41' S$  Latitude and  $124^{\circ} 47' W$  Longitude) with a 2 km scale bar. (Source: Google Earth, Europa Technologies, and DigitalGlobe (2009)). (c) Aerial Image of Minami Torishima [Marcus Island], September 2003, the most northwestern low reef island in the Pacific ( $24^{\circ} 17' N$  Latitude and  $153^{\circ} 59' E$  Longitude), with a 1 km scale bar. (Source: Google Earth and DigitalGlobe (2009)). (d) A partial aerial image of Helen Reef, one of the most western atolls in the tropical Pacific ( $2^{\circ} 54' N$  Latitude and  $131^{\circ} 51' E$  Longitude) and showing a 10 km scale bar (Source: Google Earth (2009), and DigitalGlobe (2009)).

- Restore reefs degraded by WWII construction and battles
- Treaties with neighboring developed nations to assist in enforcement of territorial seas and access to remote surveillance technology
- Establish a ocean-wide system of marine protected areas and employment opportunities for islanders to manage, monitor and restore habitats and species, and promote compatible visitation and education
- Negotiate fishery treaties and other foreign development that would be in the best interests of all the peoples and resources of Oceania

### Appendix A: Gallery of coral reefs at the margins and Equator of the Pacific Ocean

The following islands and atolls are a few of the many coral reef formations at the margins of the Pacific Ocean basin, and all are in relatively pristine states and potentially important for various aspects of climate change and ecological research.

- Kure Atoll, North Pacific, northernmost atoll in the Pacific ([Figure 21a](#))
- Clipperton Island, NE Pacific ([Figure 21b](#)), most north-eastern reef in the Pacific



**Pacific Coral Reefs: An Introduction, Figure 22** (a) Google Ocean image of the Haimahera Sea, north of New Guinea where a dozen small and two large islands cross the Equator at 129° 36' E Longitude. (Source: Europa Technologies (2009), Tele Atlas (2009), and Google Earth (2009)). (b) Google Ocean image of the Equator between several islands (Kuria, Aranuka, Abatiku, and Nonouti) in the Southern Gilbert Islands of Kiribati at Longitude 173° 49' E. (Source: Europa Technologies (2009) and Google Earth (2009)). (c) Google Ocean image of the Equator crossing northern Isla Isabela and close to the rest of the Galapagos Islands at 90° 32' W Longitude. (Source: Europa Technologies (2009), Lead Dog Consulting (2009), and Google Earth (2009)). (d) Aerial image, Dec 2007, of Kapingamarangi with a 5 km scale bar, an atoll settled by Polynesians about 600 years ago. The atoll is within 1° N of the Equator at Longitude 154° 46' E, and south of the Pohnpei State of the Caroline Islands (Source: DigitalGlobe (2009) and Google Earth (2009)).

- Ducie Atoll, SE Pacific (Figure 10), most southeastern atoll in the Pacific
- Minami Torishima (Marcus Island), NW Pacific (Figure 21c), most northwestern reef in the Pacific where Japan maintains a weather station, and
- Helen Reef (Figure 21d), one of the westernmost atolls in the Pacific

One island in the eastern border of the Pacific (Isabela in the Galapagos) and a dozen islands in the Haimahera Sea, NW of New Guinea, at the opposite end of the Pacific

support the only reefs crossing the Equator within the Pacific Ocean. Several other reefs in the Northern Phoenix, Southern Gilberts, Southern Lines, and Kapingamarangi Atoll in the Caroline Islands fall within 1° of latitude of the Equator. Some of these islands are uninhabited, many are in healthy condition, and most could serve as important sites for climate-change research.

- Jarvis Island National Wildlife Refuge (NWR), central Line Islands (Figure 15.13, in Maragos et al., 2008)



- Banaba and Nauru Islands, west of the Gilbert Islands (see Figure 9)
- A dozen Haimahera Sea islands, north of New Guinea (Figure 22a)
- Several islands in the southern Gilberts (Figure 22b)
- Isla Isabela in the main Galapagos Islands in the Eastern Pacific (Figure 22c)
- Kapingamarangi Atoll south of the Caroline Islands (Figure 22d)
- Baker Island NWR in the northern Phoenix Islands (Figure 15.11, in Maragos et al., 2008), and
- Howland Island NWR in the northern Phoenix Islands (Figure 15.12, in Maragos et al., 2008).

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## Cross-references

[Acanthaster planci](#)  
[Antecedent Platforms](#)  
[Atoll Islands \(Motu\)](#)  
[Atolls](#)  
[Barrier Reef \(Ribbon Reef\)](#)  
[Coral Cay Classification and Evolution](#)  
[Climate Change and Coral Reefs](#)  
[Daly, Reginald Aldworth \(1871–1957\)](#)  
[Darwin, Charles \(1809–1882\)](#)  
[Davis, William Morris \(1850–1934\)](#)  
[East Indies Triangle of Biodiversity](#)  
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[Submerged Reefs](#)  
[Subsidence Hypothesis of Reef Development](#)  
[Tahiti/Society Islands](#)  
[Tethys Ocean](#)  
[Vanuatu](#)

## PACKSTONE

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Packstone is a type of limestone recognized in the Dunham (1962) Classification Scheme that is grain supported and contains some sand-sized particles.

## Bibliography

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## Cross-references

[Porosity Variability In Limestone Sequences](#)

## PALAEOSOLS

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## Synonyms

Paleosols; Terra Rossa soils

## Definition

A palaeosol (or paleosol) is, as its name suggests, an old soil. The term is particularly used to describe the reddish layers, also called *terra rossa*, that occur over the surface reef limestones and within fossil dune sequences.

Soils form on subaerial exposures, such as on reef islands, or on the surface of reef limestones when these are exposed at times of lower sea level. Palaeosols, the remnants of former soils, are encountered where the soil has become lithified and has been preserved. The upper surface of reef limestones often has an incomplete cover of these former soils, together with other diagenetic evidence of exposure to terrestrial processes. These formed at times when the carbonates have been emerged, particularly during glaciations. Pleistocene reef limestones are often capped by a reddish brown crust, also called “caliche,” or calcrete, as across many of the islands in the Bahamas. A similar surface is encountered where drill cores intersect the upper surface of buried Pleistocene surfaces, as at discontinuities beneath Eniwetok, Mururoa, and Fangataufa, and on reefs on the Great Barrier Reef. These former soils are marked by micrite and sparry cements, as well as reddish-brown colouration.

On several emergent islands, such as Nauru and Niue, there are extensive deposits of phosphate that are interpreted to have accumulated from the droppings of seabirds, and which is known as guano. Phosphate-rich soils occur on some reef islands where there are presently large numbers of seabirds, and cemented phosphate deposits on Holocene-age islands are similarly considered to be the remnants of soils developed in this manner, lithified, and preserved as palaeosols.

Particularly well-developed palaeosols are associated with carbonate dune deposits. Fossil dunes, termed as aeolianite (or eolianite), are composed of sand-sized carbonate sediments, also known as calcarenite. On large calcarenite islands, such as Bermuda and the islands of

the Bahamas, the separate phases of dune accumulation are bounded by prominent red palaeosols. A lesser interruption in dune accretion is marked by a less well-developed soil horizon known as a protosol, or a hard layer of calcrete.

Palaeosols formed during periods when the dunes were stabilized by vegetation. Despite an early view that the fossil dunes formed during periods of low sea level, such as the last glacial maximum, it is now known from extensive dating on many eolianite islands that most dunes accumulated during sea-level highstands. The clay-rich palaeosols mark those periods during which the sea was lower, the glaciations. Prominent in many palaeosols are fossils of land snails, such as *Cerion* in the case of the Bahamas, and *Placostylus* on Lord Howe Island. Also widespread are the bones of seabirds, as well as rich assemblages of other fossils. Identification and dating of palaeosols and their correlation across islands enables discrimination of the intervening fossil dune formations. These sequences have been particularly effectively mapped and researched on the island of Bermuda.

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## Cross-references

[Calcrete/Caliche](#)  
[Eolianite](#)  
[Soils of Low Elevation Coral Structures](#)

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## PALEOCLIMATE FROM CORALS

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## Synonyms

Coral-climate proxies; Coral palaeoclimatology/paleoclimatology; Paleoceanography; Past climates from corals

## Definition

*Coral paleoclimatology* is the use of geochemical records from the skeletons of fossil or modern corals to reconstruct tropical climate variability during the time the coral lived.

## Introduction

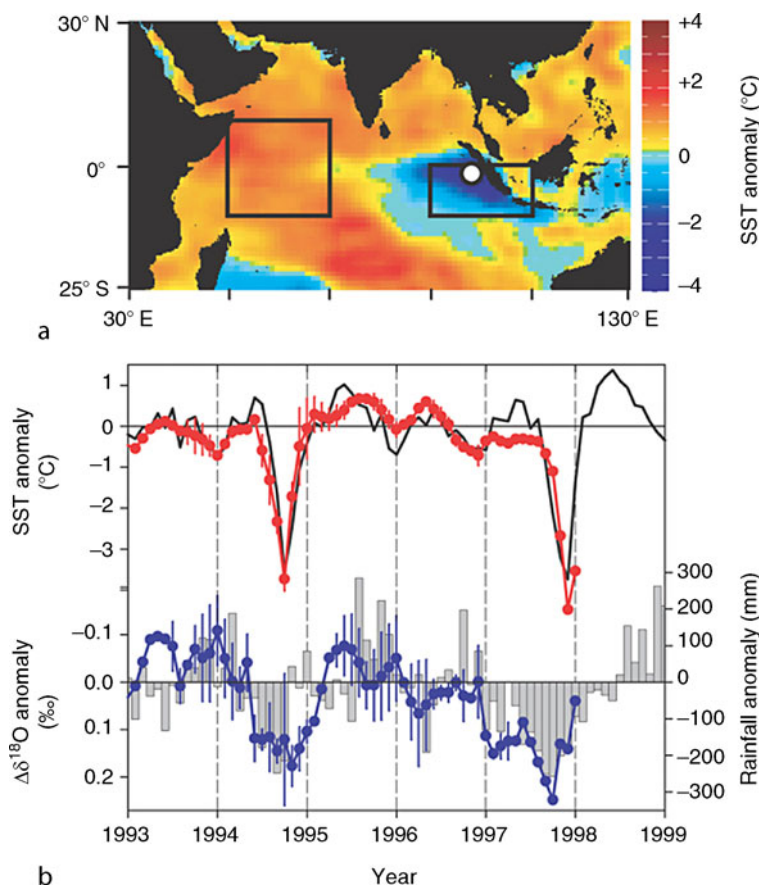
Ocean–atmosphere interactions in the tropics have far-reaching consequences for climate variability across the globe. The tropics drive heat transfer to the poles, and tropical inter-annual oscillations such as the El Niño–Southern Oscillation (ENSO) and Indian Ocean dipole (IOD), via atmospheric teleconnections, affect rainfall patterns and climate conditions in areas far beyond the tropics (Ropelewski and Halpert, 1987), causing major socio-economic impacts. Monitoring efforts have focused on improving observations and understanding of tropical climate variability, with the view to refining modeling of the tropical oceans and atmosphere. Despite these efforts, most instrumental records span only the past few decades and do not capture the full range of tropical climate variability, limiting our ability to model future changes. Coral paleoclimatology offers the prospect to extend instrumental records of tropical climate variability and can provide unique insights into tropical ocean–atmosphere interactions.

Long-lived, massive corals record climate changes in the geochemistry of their skeletons. As corals grow, they deposit an aragonitic (calcium carbonate) skeleton, usually as one high and low density band per year, visible by x-ray of the coral skeleton (Barnes and Lough, 1993). Incorporated in the coral skeletons are varying proportions of geochemical elements, depending on the prevailing environmental and climatic conditions in the ambient seawater in which the corals live, and on the coral's own physiology (see “[Stable Isotopes and Trace Elements](#)”). The geochemical, or the so-called “proxy,” records derived from the coral skeletons can be measured at sub-annual resolution and can be empirically related to a given climate parameter (e.g., [Figure 1](#)). Widely used coral proxies include the ratio of strontium to calcium (Sr/Ca), a proxy for sea surface temperature (SST), and the coral oxygen isotope ratio ( $\delta^{18}\text{O}$ ). The coral  $\delta^{18}\text{O}$  is a function of SST and the  $\delta^{18}\text{O}$  of seawater, where the  $\delta^{18}\text{O}$  of seawater correlates with changes in sea surface salinity (SSS), which in turn may respond to changes in rainfall. Using the Sr/Ca SST proxy, the SST component of the coral  $\delta^{18}\text{O}$  signal can be removed leaving the oxygen isotope residual ( $\Delta\delta^{18}\text{O}$ ) a SSS-only proxy (McCulloch et al., 1994; Gagan et al., 1998; Gagan et al., 2000). With the most commonly used coral genus *Porites* often living for a century or more, measurement of the coral skeletal geochemistry can provide quantitative, seasonally resolved, century-length records of climate variability for the time the coral lived.

## Reconstructing climate records from corals

*General approach.* There are two main approaches to reconstructing past climates from corals using modern or





**Paleoclimate from Corals, Figure 1** IOD climate anomalies. (a) SST anomalies during November of the 1997 IOD event (Reynolds and Smith, 1994), when anomalous cooling in the east and warming in the west produced a reversal of the equatorial SST gradient across the Indian Ocean. Boxes mark the eastern and western sectors used to define the dipole mode index (Saji et al., 1999), and the white circle shows the location of the Mentawai Islands. (b) In the Mentawai Islands the strong IOD events of 1994 and 1997 were characterized by cool SST anomalies (black curve; Saji et al., 1999) and drought (gray bars; Xie and Arkin, 1996). These distinct IOD SST and rainfall anomalies are preserved, respectively, in coral Sr/Ca SST (red circles and curve) and  $\Delta\delta^{18}\text{O}$  (blue circles and curve) anomalies (Gagan et al., 1998). Coral time series between July 1993 and February 1997 are based on the average of two coral records, with error bars showing the difference between the coral records for each monthly data point. (Reprinted by permission from Abram et al. [2007].)

fossil corals. The most common approach is to collect a core from a live coral on a reef. The chronology is provided from the coral density growth bands and/or the seasonal cycle recorded in the coral geochemical records. Annual coral density bands can be counted; beginning at the tissue layer at the uppermost surface of the coral, the paired high and low density bands, revealed by x-ray of the coral, are counted back in time. Coral density bands are not always well defined, so alternatively the annual peaks or troughs in the coral geochemical climate proxies can themselves be counted. Using either method, or a combination of the two, it may be possible to count back several centuries with errors of 1 or 2 years (Lough and Barnes, 1997; Guilderson and Schrag, 1999; Hendy et al., 2002; Hendy et al., 2003). The advantage of using a modern coral for climate reconstruction is that the start age is known and the coral geochemical proxies can be

directly calibrated against climate parameters as measured in the instrumental records increasing the robustness of the reconstruction. In addition, replicate coral cores can be taken from different coral heads from the same reef, enhancing reproducibility. The disadvantage is that the reconstructed record is limited by the length of time the coral lived, usually no longer than a few centuries. Dating errors may increase further back in time. There are now significant numbers of modern coral records extending back several centuries from the present day from various locations throughout the tropics such that the records are being combined to examine the climate connectivity of the tropical oceans (Kaplan et al., 1998; Evans et al., 2000; Hendy et al., 2002; Charles et al., 2003; Wilson et al., 2006).

An emerging alternative approach is to use well-preserved fossil corals to reconstruct climate further back



**Paleoclimate from Corals, Figure 2** Fossil *Porites* sp. coral from Muschu Island, Papua New Guinea. The coral, once living underwater on the reef, has been uplifted by tectonic activity and is now preserved as an isolated coral head within the intertidal zone, and is exposed at low tide. Note the concentric growth bands in this coral and that the top of the coral has been planed flat.

in time (Figure 2). The age of the fossil coral can be precisely determined using radiocarbon or U-series dating, and the proxy climate record from the coral skeleton provides a “snapshot” of past variations (e.g., Beck et al., 1997; Gagan et al., 1998; Tudhope et al., 2001; Woodroffe et al., 2003; Corrège et al., 2004; Felis et al., 2004; McGregor and Gagan, 2004; Abram et al., 2007). It is also essential to analyze a modern coral that overlaps instrumental record to quantify the coral geochemistry–climate parameter relationship since the same climate proxies are used for the fossil and modern corals. In this case, the modern records for calibration need not extend back several centuries. The major advantage of using fossil corals is that it is possible to look at climate variations further back in time when the climate boundary conditions were different from today, giving a perspective on the range of possible, natural climate modes. The disadvantage of using fossil coral proxy records is that they are almost inevitably disjointed. However, an exciting new development has been to use high-precision U-series dating of multiple fossil coral and look for age overlaps (Cobb et al., 2003; Zhao et al., 2009). Age dating errors are typically  $\pm 0.5\%$ , equivalent to less than a decade for Holocene-aged corals, and where individual fossil corals overlap in age their proxy records can be pieced together, where the climate “wiggles” from each individual coral are matched, to produce a longer record (Cobb et al., 2003).

**Coral-climate signals and reproducibility.** For both fossil and modern coral studies, it is essential to establish the climate factors controlling the signal at a given location, quantify this relationship, and determining the magnitude of associated errors. For example, the commonly used  $\delta^{18}\text{O}$  proxy reflects changes in both SST and SSS. However at some locations, such as in PNG in the western tropical Pacific SSS changes dominate the signal (Tudhope et al.,

2001; McGregor, 2004), whereas at locations such as the central Pacific SST exerts the major control (Evans et al., 2000; Woodroffe and Gagan, 2000). In addition, the aim for coral paleoclimatology is often to be able to use the coral proxy record from a single location to infer regional climate variability. Thus, the climate factors that control the coral proxy climate signal must be quantifiably related to regional climate variations (Guilderson and Schrag, 1999). Some locations appear to be “nodes” for particular tropical climate oscillations (e.g., ENSO or the North Atlantic Oscillation), and coral records from these locations can be representative of climate variability over very large spatial areas. One example of this is where coral-climate records from Kiritimati Island were used to construct a coral-C INDEX, equivalent to the NINO3.4 Index used to define ENSO events (Evans et al., 1998). From this point of view, corals from well-flushed reef settings are preferred. For in situ fossil corals it is usually possible to establish the paleo-reef morphology; however, for transported corals (dislodged either by storm activity or post-uplift erosion) establishing provenance is almost impossible (Cobb et al., 2009).

Several studies have suggested that proxy climate signals from corals living on the same reef may show higher between-coral (inter-reef) differences than that expected from climate variability alone (Guilderson and Schrag, 1999; Linsley et al., 1999; Cohen et al., 2002; Felis et al., 2003). The origins of these offsets are not well understood, and, in addition, there are studies that suggest minimal between-coral offsets (Gagan et al., 1998; Hendy et al., 2002; Stephans et al., 2004). But between-coral differences appear to affect the coral oxygen isotope ratios more than Sr/Ca. Coral growth form, growth rate, reef setting, and diagenesis have all been suggested as possible causes of offsets (Cobb et al., 2009). Corals can also show within-coral variations (McConnaughey, 1989; de Villiers et al., 1995; Alibert and McCulloch, 1997; Cohen and Hart, 1997). Regardless of the origin and magnitude of between-coral and within-coral offsets, reproducing proxy climate signals from the same location, using at least two corals, will reduce uncertainty and quantify errors in climate reconstructions from both modern and fossil corals (Lough, 2004; Stephans et al., 2004; Abram et al., 2009).

**Diagenesis.** An underlying assumption in the use of corals to reconstruct climate is that the corals are pristine, that is, that original coralline aragonite is preserved. However, coral skeletons are susceptible to a process known as diagenesis. Diagenesis is the precipitation of secondary aragonite or calcite in skeletal voids, or the replacement of skeletal aragonite, usually with calcite. If even a small amount of diagenetic material is included in a sample, then the resulting climate reconstruction may be rendered inaccurate. This is because isotopes and trace elements are exchanged and removed during the diagenetic transformation, changing the geochemistry of the coralline matrix. For example, secondary calcite can lead to “warm” SST artefacts (SST appears warmer than was the case), particularly in Sr/Ca SST reconstructions, of  $1^\circ\text{C}$  or more

(McGregor and Gagan, 2003). Secondary aragonite, typical for early marine diagenesis of modern corals, causes considerable alteration of coral geochemistry and creates “cool” SST artefacts (Bar-Matthews et al., 1993; Enmar et al., 2000; Müller et al., 2001; Lazar et al., 2004; Müller et al., 2004; Allison et al., 2007). Dissolution was shown to create “cool” anomalies in a range of trace element SST proxies (Hendy et al., 2007). Diagenesis has been observed in living corals and corals just a few decades old (Enmar et al., 2000; Müller et al., 2001; Hendy et al., 2007; Nothdurft et al., 2007); however, fossil corals are more susceptible to diagenetic processes as they are exposed to seawater, sea spray, rainfall, and/or groundwater for centuries to millennia or longer.

Numerous studies have called for screening for diagenesis in modern and fossil corals to become standard procedure (McGregor and Gagan, 2003; Gagan et al., 2004; Quinn and Taylor, 2006; Allison et al., 2007; Hendy et al., 2007; Cobb et al., 2009). Diagenesis that produces an addition of ~10% or more secondary material to the skeletal bulk density can be detected in coral density profiles, X-radiographs, and UV luminescence photos (Hendy et al., 2007). However, just 1% calcite diagenesis would alter the coral climate signal (McGregor and Gagan, 2003). X-ray diffraction (XRD) has been the most commonly used diagenesis screening method in coral paleoclimate studies. However, XRD detects secondary calcite, not secondary aragonite or dissolution, and the XRD detection limit is effective down to around the 1% calcite (McGregor and Gagan, 2003; Allison et al., 2007). For lower levels of diagenesis, thin section is proving a highly effective means of screening samples for all types of diagenesis (McGregor and Gagan, 2003; McGregor and Abram, 2008; Cobb et al., 2009). One thin section per 20–30 years of coral growth is recommended (Cobb et al., 2009) and a guide has been developed to assist coral paleoclimatologists in screening using thin sections (McGregor and Abram, 2008). Scanning electron microscopy (SEM) is also a highly effective tool for diagenetic screening (Nothdurft et al., 2007).

### Coral paleoclimate records

One of the major strengths of corals as paleoclimate archives is their ability to record monthly or finer resolution (e.g., weekly) climate information. This level of resolution means corals are ideally suited to investigating inter-annual climate phenomena, such as the El Niño–Southern Oscillation and the Indian Ocean Dipole. Approximately 90 coral proxy records based on corals that were alive at the time of collection have been published, with around 30 of those extending from the late twentieth century back prior to 1900 (Jones et al., 2009). These longer coral records are able to provide a wealth of information on multidecadal to centennial timescale variability. At least one coral record exists from every tropical ocean, with the vast majority of records from the tropical Pacific. There are significantly fewer records from

older fossil corals. Coral paleoclimatology has made a significant contribution to understand a number of facets of tropical climate variability and a snapshot of these contributions will be discussed in the following sections.

### Interannual and multi-decadal variability in the tropical Pacific: variations past and present

A key focus of coral paleoclimate research has been in extending records of the El Niño–Southern Oscillation system. ENSO, with its origins in the equatorial Pacific, is the largest source of interannual climate variability across the planet. It is a coupled climate system between the atmosphere and the ocean, and it oscillates irregularly on a timescale of 2–7 years. The average state of the equatorial Pacific Ocean involves strong easterly trade winds pushing warm water to the west, which then brings (upwells) cool subsurface water in the east. This sea surface temperature gradient then reinforces the easterly winds. A La Niña event is an enhancement of the average state, where the easterly winds and temperature gradient strengthen. In an El Niño event, the easterly winds slacken and reduce the ocean temperature gradient, allowing warm water to flow back to the central and eastern Pacific. Atmospheric convection and precipitation follows the warmest water, and in an El Niño, above average rainfall is deposited over the central Pacific. El Niño events have become stronger and more frequent since the mid-1970s (McPhaden et al., 2006). However, there is debate about whether strengthened El Niño is a result of global warming or whether the 1970s intensification resulted from a decadal or longer-term cycle of ENSO variability (Fedorov and Philander, 2000; Cane, 2005; McPhaden et al., 2006). The relatively short instrumental record does not give a complete picture of ENSO behavior, and models are unable to simulate ENSO fully, limiting our ability to predict future ENSO scenarios.

Corals from optimal locations across the equatorial Pacific are able to capture the SST and rainfall/SSS variations that result from ENSO oscillations (Cole et al., 1993; Dunbar et al., 1994; Evans et al., 1998; Urban et al., 2000), and have complemented and extended instrumental records of ENSO variability. Spectral analysis of one of the earliest published coral  $\delta^{18}\text{O}$  records, that from Tarawa Atoll, western Pacific, showed changing dominance of seasonal and interannual variability through the twentieth century, suggesting a change in the ENSO “pulse” (Cole et al., 1993). Further analysis of the Tarawa  $\delta^{18}\text{O}$  record and comparison with a 155 year  $\delta^{18}\text{O}$  record from Maiana Atoll, just south of Tarawa, revealed, among other things, that the 1976 shift in ENSO variability coincided with changes in the mean background climate of the tropical Pacific, with the ENSO period shifting from 2.9 to 4 years across the 1976 change (Urban et al., 2000). The record also revealed that during the late nineteenth century, ENSO cycles lasted 10–15 years. These results are significant because they show that the length of the ENSO cycle varies with small changes in tropical climate.



Furthermore, the results suggest that there is substantial natural variability in ENSO, but that the most recent period may be unique in that the changes in the mean climate due to anthropogenic greenhouse gases may also influence ENSO (Dunbar, 2000).

The network of coral-climate records from across the Pacific, although still sparse, does appear to capture large-scale, multi-decadal climate variance, and in combination with coral records from other ocean basins, is revealing ocean-atmosphere connections right across the tropics. Consensus is emerging for significant decadal variability in tropical Pacific SSTs at the 9–14 year period (Cobb and Charles, 2001; Holland et al., 2007; Ault et al., 2009). The decadal variability displays an ENSO-like spatial and temporal pattern suggesting that the Pacific decadal-scale variance is directly related to ENSO (Urban et al., 2000; Holland et al., 2007; Ault et al., 2009). Decadal-scale variability appears to be stronger in the late nineteenth century, and analysis based on only twentieth century records may underestimate decadal-scale variability (Ault et al., 2009). Synthesis of coral SST records spanning the whole tropics suggests that the late twentieth century is the warmest period for the past 250 years, which can be explained by the increase in anthropogenic greenhouse gases in the atmosphere (Wilson et al., 2006). A consistent antiphased correlation between the South Pacific Convergence Zone, a low pressure trough extending from around the Solomon Islands to French Polynesia, and the decadal variability in the central equatorial Pacific has been documented back to 1650 AD (Linsley et al., 2008). At the decadal-scale the Atlantic Ocean may be directly influenced by SST anomalies in the central tropical Pacific (Cobb and Charles, 2001), and central equatorial Pacific SSTs also correlate on a variety of timescales with Indian Ocean coral oxygen isotope records, suggesting a decadal-scale connection between these ocean basins (Cobb and Charles, 2001; Charles et al., 2003).

The longest, continuous coral proxy record published to date, based on eight coral cores from the Great Barrier Reef (GBR), sampled at 5-yearly resolution and totaling 420-years from present back to 1565 AD, showed that corals can also record centennial-scale shifts in tropical climate (Hendy et al., 2002). This study was unique in its approach in that it combined records in a similar manner to the approach used in tree-ring studies to extract the robust “common signal” of low-frequency SST and SSS variability in the records. The resulting common GBR SSS anomaly record showed increased salinity between 1565 and 1870, around the time of the Little Ice Age (LIA) in the northern Hemisphere (Hendy et al., 2002). The SST anomaly results, along with other long records from the tropical Pacific, suggest a stronger latitudinal temperature gradient during the LIA, enhancing wind-driven evaporation, giving rise to the high salinity anomalies. The authors suggest that the high evaporation equated to a net export of moisture from the tropics contributing to glacial advance during the LIA (Hendy et al., 2002).

Also, drawing on approaches adapted for tree-ring studies, Cobb et al. (2003) pieced together numerous fossil and modern corals from ENSO-sensitive Palmyra Atoll, central Pacific, to give the first picture of ENSO variability for the past millennium. Their landmark reconstruction was based on dislodged coral heads deposited on Palmyra during storms events. The corals were precisely dated by the U-Th method to identify periods of overlap, and then the monthly resolved  $\delta^{18}\text{O}$  records were “wiggle matched” together. In total, this resulted in 430 years of monthly resolved record, for five intervals across the past millennium. The record showed a surprising degree of variability in ENSO strength, independent of changes in solar or volcanic forcing. In addition, ENSO strength does not appear to relate to changes in Northern Hemisphere climatic periods such as the Little Ice Age or Medieval Warm Period (Cobb et al., 2003). ENSO strength seemingly switches modes in a matter of decades, and the late twentieth century ENSO, although strong, is not unprecedented over the length of the record (Cobb et al., 2003). The results suggest that ENSO can change its character on its own, and in future, may shift with or without an additional push from anthropogenic greenhouse gases (Cobb et al., 2003; Tudhope and Collins, 2003). This presents a challenge for modeling future ENSO behavior, and testing global climate models against past ENSO variability provides a means to refine and improve these models.

Coral paleoclimate reconstructions have been instrumental in understanding the origin and long-term evolution of ENSO (Hughen et al., 1999; Corrège et al., 2000; Tudhope et al., 2001; Woodroffe et al., 2003; Kilbourne et al., 2004; McGregor and Gagan, 2004; Sun et al., 2005). A major discovery from Indonesian and Papua New Guinea (PNG) fossil corals has been that ENSO has been a component of the tropical climate system for at least 130,000 years (Hughen et al., 1999; Tudhope et al., 2001), and has varied significantly in strength through glacial and interglacial cycles (Tudhope et al., 2001). Tudhope et al. (2001) proposed that ENSO strength varied as a result of changes in tropical Pacific seasonality related to the Earth’s orbital cycles (orbital forcing) plus dampening of ENSO strength during glacials. Further work on coral from PNG, and additional coral records from the central Pacific, are providing a more detailed picture of the evolution of ENSO for the most recent Holocene period (10,000 years ago to present; Corrège et al., 2000; Tudhope et al., 2001; Woodroffe et al., 2003; Gagan et al., 2004; McGregor and Gagan, 2004; Sun et al., 2005). These studies suggest that ENSO was less active compared to today, although still present, and may have been more active around 2,000 years ago.

A key component of ENSO and the tropical Pacific climate system is the Indo-Pacific Warm Pool (IPWP). The IPWP is the warmest body of ocean water in the world having an average temperature of  $>28^{\circ}\text{C}$ , and coupled ocean-atmosphere interactions in the IPWP are not only thought to trigger El Niño events, but also deliver large

amounts of heat to the atmosphere via the global atmospheric Hadley-Circulation (Webster, 1994). Much coral evidence for the evolution of ENSO originates from the IPWP and coral data has also provided important information on the long-term climate variability of the warm pool. Sea surface temperature estimates, based on corals from Vanuatu, PNG, GBR, and Indonesia and utilising a revised coral Sr/Ca SST calibration, suggest that the early Holocene IPWP was  $\sim 1\text{--}3^\circ\text{C}$  cooler than present (Gagan et al., 2004 and references therein). Temperatures had reached modern values by  $\sim 8.5$  ka, in general agreement with planktonic foraminifera Mg/Ca and alkenone SST estimates, and mid-Holocene SSTs were  $0.5\text{--}1^\circ\text{C}$  warmer than present (Gagan et al., 2004). A more detailed picture of IPWP SST variations, based on 48 fossil corals from Indonesia and PNG, suggested that the southern margin of the IPWP cooled and warmed periodically through the mid-Holocene, associated with an expansion and contraction of the warm pool as the Asian summer monsoon weakened and strengthened, respectively, and points to the fundamental importance of the warm pool in propagating climate change (Abram et al., 2009).

### Interannual modes in the Atlantic and Indian Ocean

Understanding the influence of the tropical Pacific and ENSO on the Indian Ocean has been recognised as an important issue and corals have played a role in better characterising the interactions. For the past few decades, SSTs in the Indian Ocean have been associated with ENSO and the Asian monsoon via complex multi-feedbacks (Webster et al., 1998). As with the tropical Pacific, however, a major limit in understanding climate variability in the tropical Indian Ocean, and the Indian, East African, and southeast Asian monsoons, on which millions of people are dependent for life-giving rain, has been the absence of records of more than a few decades in length. Multi-century coral oxygen isotope records from the central and western Indian Ocean however, reveal a clear ENSO teleconnection, whereby during El Niño events western Indian Ocean SSTs are warmer (Charles et al., 1997; Cole et al., 2000; Zinke et al., 2005; Pfeiffer and Dullo, 2006). The western Indian Ocean SSTs also display decadal-scale ENSO-like variability (Cole et al., 2000; Pfeiffer and Dullo, 2006), which may be linked to the Pacific decadal oscillation (Crueger et al., 2009).

Although there may be a generally consistent teleconnection between the western Indian Ocean and ENSO, new perspectives from coral records from the eastern Indian Ocean show a changing ENSO–Indian Ocean–monsoon interaction, with potentially negative consequences for SE Asian rainfall under global warming scenarios (Abram et al., 2007). Recently identified IOD events are defined by a reversal of the equatorial Indian Ocean east–west SST gradient and zonal winds from their mean climatological state (Saji et al., 1999; Figure 1),

resulting in drought for western Indonesia and southern Australia (Overpeck and Cole, 2007). IOD events were reconstructed back to 1846 using a suite of corals from the eastern and western Indian Ocean (Abram et al., 2009). The coral IOD index showed an increase in the strength and frequency of IOD events through the twentieth century (Figure 1). The results also showed that despite the historical influence of ENSO in triggering IOD events, the twentieth century IOD intensification was a direct result of IOD–monsoon feedbacks, with consequences for rainfall distribution (Abram et al., 2009).

Coral reconstructions of Holocene IOD events have likewise revealed changes in the IOD–monsoon–ENSO relationship over time (Abram et al., 2007). The results are significant, their strength being that they provide information on monthly scale timing and duration of individual IOD events (Figure 1), and show that  $\sim 6,500$  years ago IOD SST cooling lasted 5 months, up from 3 months for the present day. They also reveal that long-duration IOD events result in drought peaking later in the calendar year than for the present day, coinciding with what would normally be the maximum monsoon rainfall in western Indonesia. The mid-Holocene enhanced IOD cooling and drying is thought to result from strengthened Asian monsoon, and future Asian monsoon–IOD strength may extend drought through Australasia (Abram et al., 2007).

Coral records are making a significant contribution to our understanding of the Atlantic Multidecadal Oscillation (AMO), hurricane activity, and the North Atlantic Oscillation/Arctic Oscillation (NAO/AO). The AMO is a decadal- to multidecadal-scale variation in SSTs across the Atlantic and may be related to hurricane activity in the northern tropical Atlantic (Goldenberg et al., 2001). A 440-year growth rate SST reconstruction from the Bahamas suggests that multidecadal variability may only be significant after 1730, limiting the accuracy of decadal climate forecasts (Saenger et al., 2009). In a related study, luminescence lines from Caribbean corals were used in combination with a marine sediment core proxy record to investigate hurricane frequency, vertical wind shear, SST, and the AMO for the past 270 years (Nyberg et al., 2007). The results suggest that vertical wind shear is more important than SST in controlling hurricane frequency, and controversially, that increased hurricane frequency since 1995 is not unusual compared to other periods of high hurricane activity in the record (Elsner, 2007; Nyberg et al., 2007; Neu, 2008; Nyberg et al., 2008).

Coral records, particularly those from fossil corals, have made key inroads into our understanding of the NAO/AO. The NAO/AO is the dominant interannual atmospheric mode in the North Atlantic influencing the climate of much of Europe via its modulation of the strength of the subpolar westerlies (Hurrell, 1995; Thompson and Wallace, 2001). Oxygen isotopes in corals from the northern Red Sea reflect the influence of the NAO/AO and ENSO on the climate of the region (Felis et al., 2000). Sr/Ca SST records from 125,000 year old fossil corals show increased temperature seasonality

(Felis et al., 2004). In an innovative approach, combining the seasonal-resolution coral data with coupled atmosphere–ocean model simulations, the results suggest that a more positive NAO/AO operated 125,000 years ago contributing to the increased seasonality in the Red Sea coral record, as a response to insolation changes from differences in Earth's orbital configuration at that time (Felis et al., 2004). Such studies help to disentangle natural climate variability and will help us better understand the response of interannual climate oscillations to anthropogenic greenhouse warming.

## Summary

Corals are proving an invaluable source of quantitative data on past climate variability across the tropical oceans, and over a range of timescales from seasonal, interannual, decadal to centennial and millennial. Community wide efforts to extract records from undersampled time periods, such as the LGM and deglaciation (Expedition 310 Scientists, 2006; Webster et al., 2009), and locations, and further integration of coral data and climate model output will continue to see coral paleoclimatology contribute to understanding natural climate variability.

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## Cross-references

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## PATCH REEFS: LIDAR MORPHOMETRIC ANALYSIS

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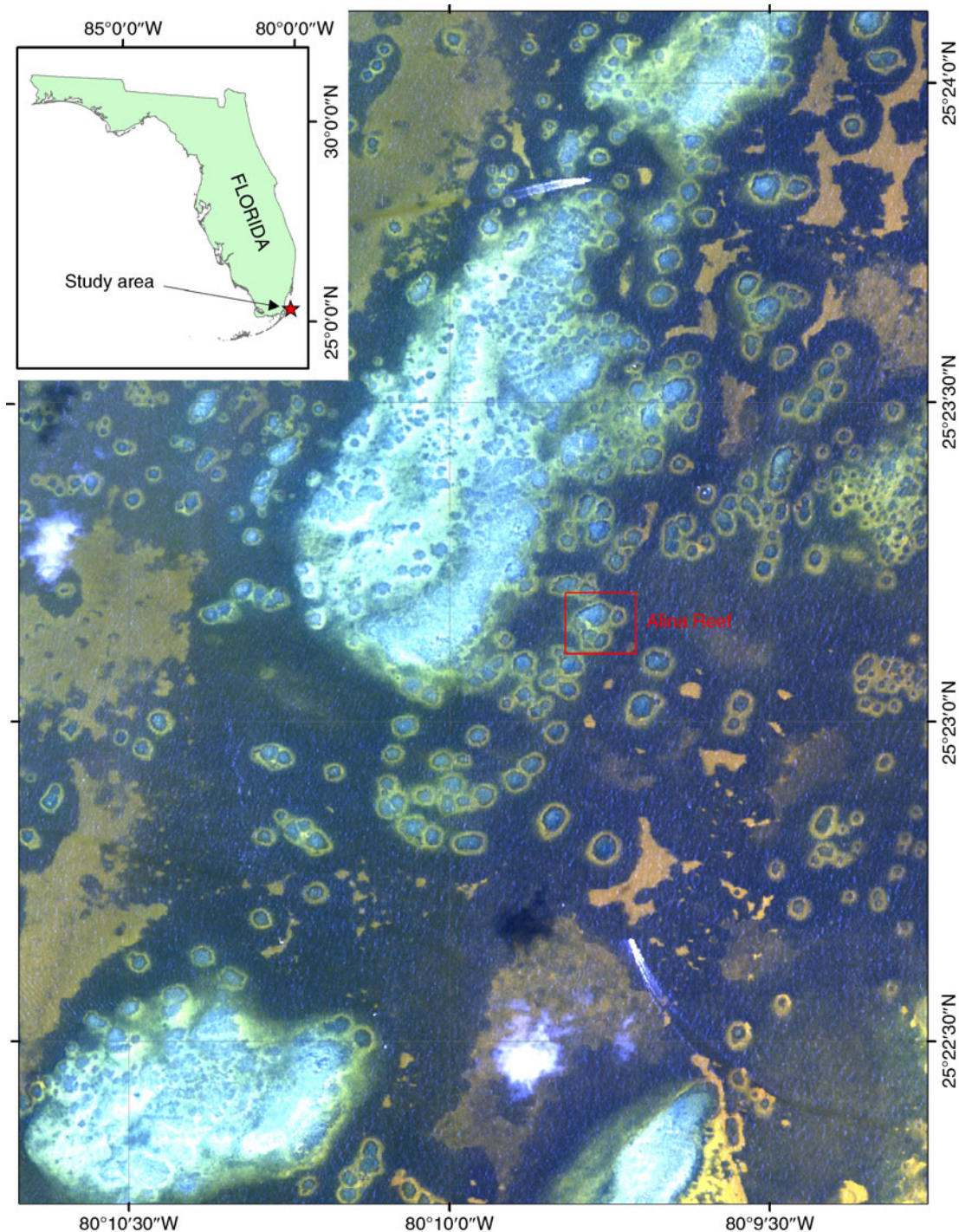
<sup>2</sup>U.S. Geological Survey, St. Petersburg, FL, USA

## Setting

Alina Reef is one of several thousand patch reefs that lie across the shallow carbonate platform seaward of Hawk Channel off the northern Florida Keys. The site is near the northern latitudinal fringe of the late Holocene western Atlantic coral reef distribution ([Figure 1](#)). The area is covered by calcareous sand and discontinuous *Thalassia testudinum* seagrass meadows and is studded with numerous scattered Holocene patch reefs. Most of the patch reefs are found in water depths of 2–9 m, are subcircular, elliptical, or irregular in plan view, and range up to about 8 m in vertical relief and 700 m in width. Coring has demonstrated thicknesses of 4.5–6 m and has revealed frameworks built by large, massive head corals.

## Lidar surveys

In August 2002, the Experimental Advanced Airborne Research Lidar (EAARL) system was used by NASA and the U.S. Geological Survey to survey the submarine topography of the broad swath of the reef tract seaward of Elliot Key and within Biscayne National Park ([Figure 1](#)). The NASA – USGS Airborne Lidar Processing System (ALPS) was used to interpret the EAARL laser soundings to create a spot-elevation data set that was subsequently subjected to triangulation and gridding to create a digital-elevation model (DEM) at 1-m cell resolution. Next, a 1-m-resolution slope map was constructed from the lidar-derived DEM based upon



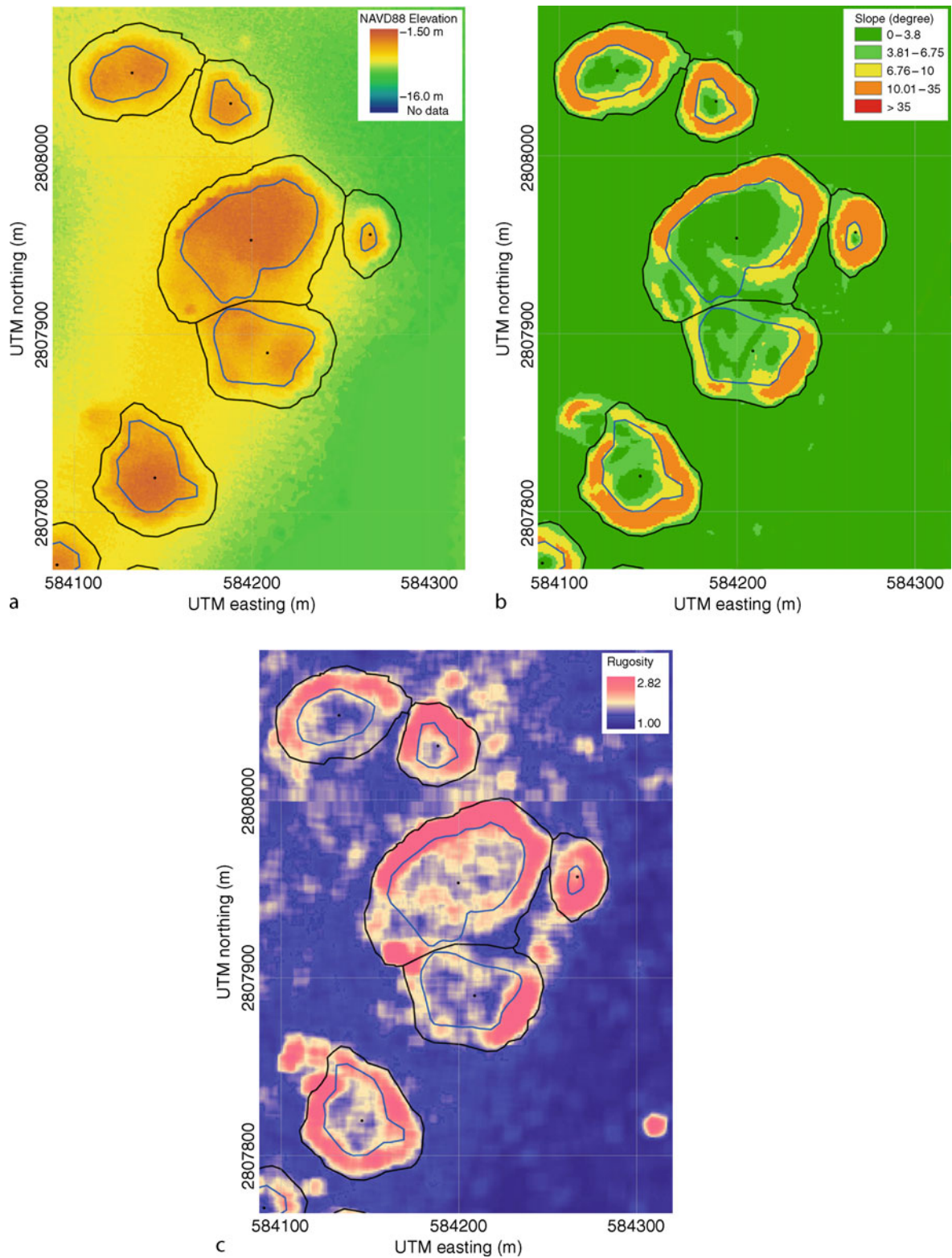
**Patch Reefs: Lidar Morphometric Analysis, Figure 1** The northern Florida Keys reef tract depicted on a QuickBird satellite image.

the average maximum method (Burrough and McDonell, 1998). Lastly, a lidar-rugosity mapping procedure was applied to produce a 1-m-resolution digital rugosity map for the study area (Brock et al., 2006).

### Morphometric analysis

The results of the lidar morphometric analysis at Alina Reef are shown in Figure 2. Alina Reef is depicted on the color-coded digital-elevation map (DEM) as the





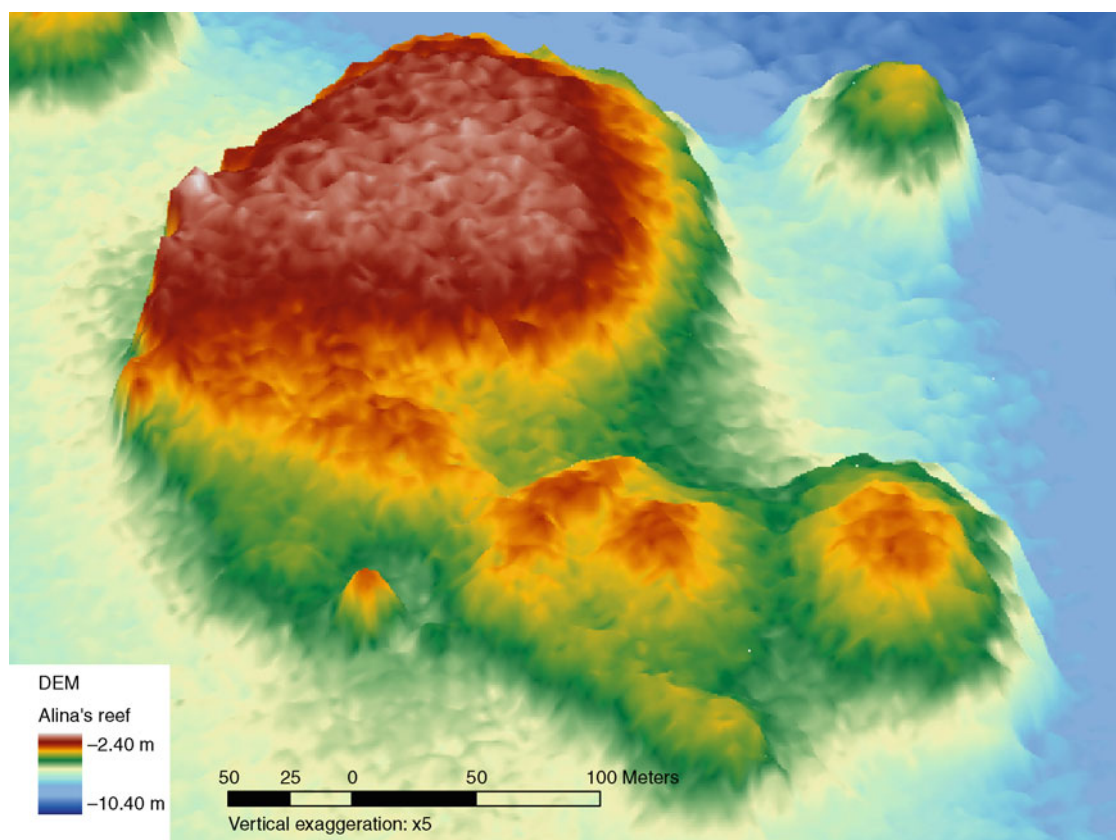
**Patch Reefs: Lidar Morphometric Analysis, Figure 2** A subregion of the 1-m-resolution lidar-based (a) topographic, (b) slope, and (c) rugosity maps that were used to define patch-reef boundaries and morphometric attributes. *Black polygons* depict boundaries of the full patch reef, *blue polygons* delimit patch-reef tops, and the area between these polygons on a given reef represents the patch-reef rim.

largest of several surrounding patch reefs at the approximate center of a small subarea of the total region mapped by the EAARL (Figure 2a). The black dots signify the volumetric center points of the patch reefs, one example of the morphological metrics that may be obtained through quantitative analysis of the lidar DEM.

An extensive morphometric analysis across the entire EAARL survey region revealed two morphologically different populations of patch reefs associated with two distinct depth intervals. Alina Reef is an excellent example of an identified group of shallow patch reefs that are generally much broader and flatter than the deeper population. Compared to the shallow reefs, the deep reefs were smaller in area and volume and showed no trend in topographic complexity relative to water depth. The fundamentally different morphologies of the shallow and deep reefs can be clearly seen on the slope map, (Figure 2b) which depicts a small steep-sided deep reef immediately adjacent and to the east of Alina Reef. The slope map also reveals scattered small rubble piles just off the western flanks of several reefs that may stem from the frequent hurricane crossings that impact the northern reef tract.

The roughly 200 m  $\times$  300 m region around Alina Reef mainly contains reefs that are members of the shallow-reef population, revealed by the lidar to be, in comparison to the deep-reef group, more variable in area and volume. Moreover, lidar revealed that reefs in the shallow population became flatter and less topographically complex with decreasing water depth.

The more uniform knoll-like morphology of the deep reefs is consistent with steady and relatively rapidly rising early Holocene sea level that may have restricted the lateral growth of reefs. The morphology of shallow “pancake-shaped” reefs (Figure 3) at the highest platform elevations may have been produced by cycles of growth and erosion driven by fluctuating sea level during the late Holocene (Balsillie and Donoghue, 2004). Although the ultimate cause for the morphometric depth trends sensed by lidar remains speculative, these interpretations are compatible with a recent eustatic sea-level curve that hindcasts fluctuating late Holocene sea level (Siddall et al., 2003). It is thus suggested that the morphological differences revealed by lidar represent two stages of reef accretion that occurred during different sea-level conditions.



**Patch Reefs: Lidar Morphometric Analysis, Figure 3** Oblique perspective topographic depiction of Alina Reef, a shallow patch reef that exhibits the characteristic “pancake” morphology of the shallow patch-reef population in the northern Florida Keys reef tract.

## Summary

Apart from providing evidence for oscillating late Holocene sea level, lidar mapping provided new information on regional reef ecology and benthic community structure. Previous work has shown that many patch reefs in Biscayne Bay are composites of several characteristic zones, namely (a) massive boulder-coral colony clusters, (b) a zone of scattered massive corals with abundant octocorals, and (c) peripheral rubble zones (Ginsburg et al., 2001). The cluster zones occur at the patch-reef margins and are mainly composed of 1–5 m-diameter coalesced colonies of *Montastraea annularis* and *Montastraea faveolata*, along with fewer *Siderastrea siderea* and *Colpophyllia natans* heads. The octocoral zone is basically a hard ground community with areas that are dominated by coral rubble and carbonate sand. The tropical storms and hurricanes that frequently track across the northern reef tract have been implicated in the formation of the rubble aprons that occur at the peripheries of many patch reefs and can readily be identified on the lidar-based slope map (Brock et al., 2006) (Figure 2b).

Analysis of dense lidar-elevation soundings can also yield spatially continuous maps of coral reef topographic complexity, or rugosity. A lidar-based rugosity map (Figure 2c) for the Alina Reef region confirms previous work that established that the known characteristic zonation of Biscayne Bay patch reefs can be sensed remotely and mapped by the EAARL system (Brock et al., 2006). The high-rugosity flanks of Alina Reef and neighboring reefs generally correspond to cluster zones of live or degraded massive boulder-coral colony clusters, or derivative rubble piles. The mixed, low-rugosity upper platforms of these reefs were identified by field observations to represent octocoral zones. In summary, the EAARL lidar reef-mapping test conducted across a portion of the northern Florida Keys reef tract, and the sample presented here, demonstrated that lidar mapping can provide new and valuable information to reef-resource managers, carbonate geologists, and coral reef ecologists.

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## Cross-references

[Florida Keys](#)  
[Postglacial Transgression](#)  
[Remote Sensing](#)  
[Swathe Mapping](#)

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## PERMIAN CAPITAN REEF SYSTEM

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The Permian Capitan Reef system (275–255 Myr), as exposed in the Guadalupe and Delaware Mountains of the Delaware Basin in New Mexico and west Texas, presents some of the finest outcrops of ancient reef and associated rocks known. Ochoan evaporites, infilled the Delaware Basin preventing extensive erosional modification and structural deformation, so preserving an entire depositional system from the back-reef across the reef margin to the deep basin.

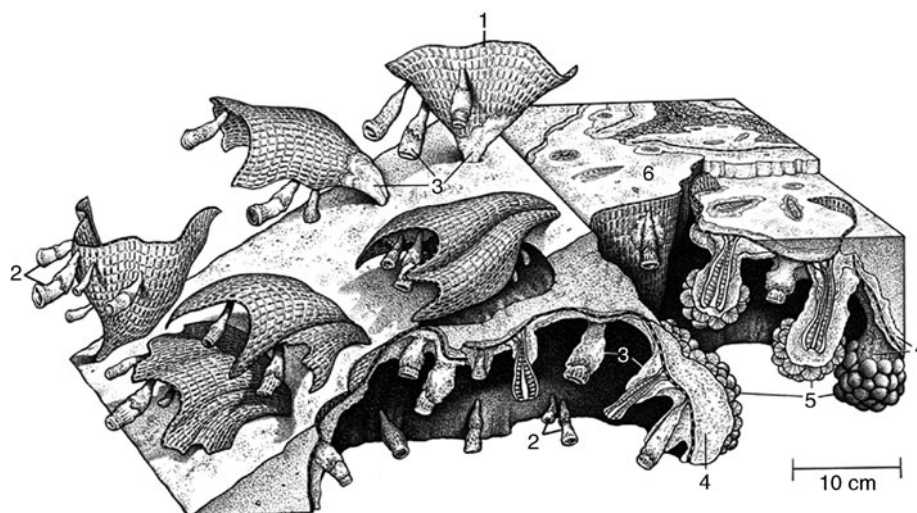
The Delaware Basin was situated close to the western margin of Pangaea, about 10° north of the palaeo-equator and was subjected to subsidence resulting in the accumulation of between 2,100 and 4,200 m of clastic, carbonate, and evaporite strata; 1,000 m alone was deposited during Guadalupian times.

The depositional system can be broadly divided into back-reef, shelf margin, reef-slope and basin sediments. Leonardian and early Guadalupian strata show shelf-to-basin ramp sequences, but these later evolved into a rimmed shelf where the margin was poised nearly 600 m above the basin floor. Topography was further enhanced by reciprocal sedimentation where considerable thicknesses of carbonates were deposited on the shelf area during transgressions and highstands, and clastic material accumulated in the basins during lowstands.

Cyclic sedimentation is widespread in the Permian Basin and operated on many frequencies. Eustatic cycles of roughly a million years or less were superimposed on an apparently long-term drop in sea level throughout late Permian time.

The Capitan reef shows a high biodiversity and is the main Guadalupian carbonate-producing facies, forming a clearly defined, largely continuous margin which surrounds the Delaware Basin. Many different reef-building communities have been documented, including various calcareous sponge-bryozoan assemblages, and phylloid algae (Newell et al., 1953). Some have re-interpreted the previously described reef framework as having lived within cavities (Wood et al., 1996). Many organisms, commonly still found in living position, are often encrusted by possible red or blue-green algae, particularly *Archaeolithoporella* as well as microbialite, which almost certainly represents secondary growth during burial (Figure 1). In addition to framework and encrusting





**Permian Capitan Reef System, Figure 1** Reconstruction of bryozoan-sponge community, Permian Capitan Reef, USA (courtesy J. Sibbick); 1. Frondose bryozoans, 2. Solitary sphinctozoan sponges, 3. *Archaeolithoporella* (encrusting alga), 4. Automicrite, 5. Syndepositional cement botryoids, 6. Sediment.

organisms, the reefs contain diverse echinoderms, bryozoans, brachiopods, molluscs, ostracodes, scarce solitary corals and trilobites. On the shelfward side of the reef, sponge-algal rubble passes into *Tubiphytes* thickets, and *Mizzia* and *Macroporella* green algal grainstones with bellerophont gastropods.

Late Guadalupian reefs and near-back-reef grainstones are filled with large volumes of syndepositional marine cements (Mazzullo and Cys, 1977). Many reef cavities were rapidly filled with massive botryoids and radial-fibrous cements, partly intergrown with *Archaeolithoporella* and internal sediment.

High rates of biological productivity produced more carbonate than could be accommodated given limited rates of subsidence and, excess material was transported into back-reef and particularly fore-reef environments. As a result, the Capitan reef shows considerable seaward progradation, varying from 10 km on the stable western margin of the Delaware Basin to 3 km on the more rapidly subsiding eastern margin (Ward et al., 1986).

The rapid rates of syndepositional cementation of the reef facies combined with progradation over largely unconsolidated and compactable debris, led to extensive syndepositional fracturing of the cemented reef slabs and differential subsidence of the reef complex as a whole (Saller, 1996).

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## Cross-references

[General Evolution of Carbonate Reefs](#)

## PERSIAN/ARABIAN GULF CORAL REEFS

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## Definition

The Persian/Arabian Gulf (herein referred to as the "Gulf") is a subtropical, epicontinental sea situated roughly between 23°50'N and 29°52'N and is therewith home to some of the northernmost coral reefs on the western boundary of the Indo-Pacific (Kharku Island, Iran, at

29°20'N). The Gulf is 989 km long and 50 km wide and has an area of 251,000 km<sup>2</sup>. It has an average depth of 20 m and a maximum of 90 m. Its shallow nature, combined with the high-latitude geographical position and the presence of mountainous plateaus and deserts nearby, make the Gulf's climate the most extreme endured by reef-building corals anywhere in the world. Nonetheless, the Gulf is home to about 40 species of scleractinian and 31 species of alcyonacean corals. The reef fauna represents a small but typical segment of that of the Indo-Pacific.

### The distribution of coral reefs in the Gulf

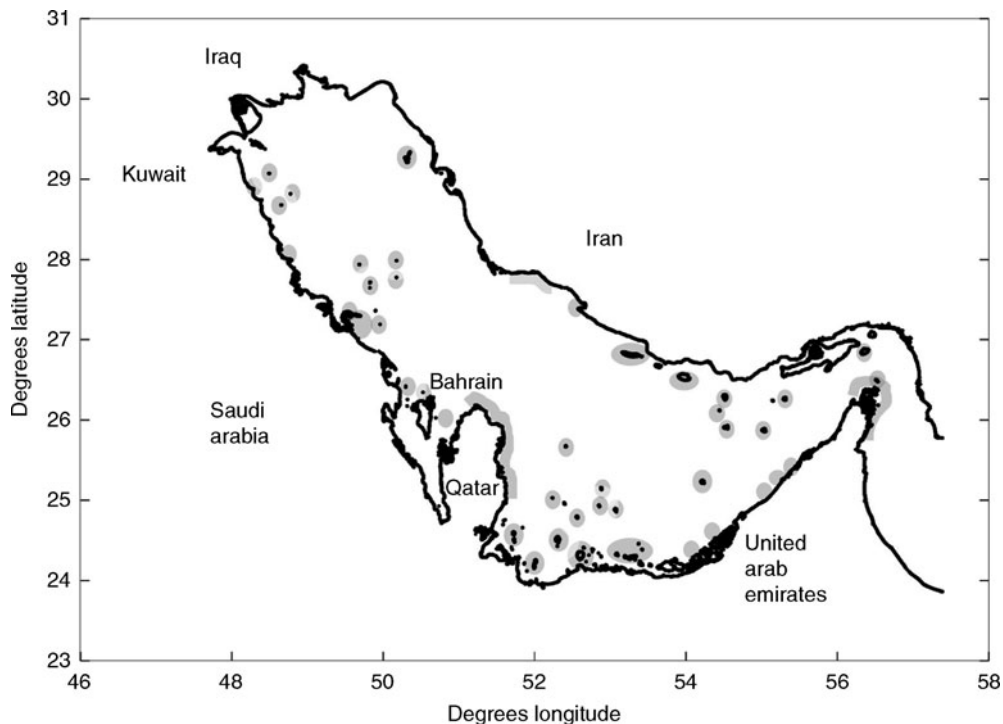
Coral growth occurs virtually throughout the entire Gulf (Figure 1), with best development on offshore shoals but important fringing systems even along the mainland shoreline (in particular, UAE, Qatar, Saudi Arabia). Relatively few records exist of coral assemblages on the Iranian mainland coast (Shokri et al., 2000; Maghsoudlou et al., 2008), which can be due to runoff from the mountainous hinterland creating unfavorable conditions as well as insufficient records in the literature available in the West. Pleistocene (MIS 7 and 5e) reefs are known from the Iranian islands of Kish (Preusser et al., 2003) and Qeshm (Pirazzoli et al., 2004).

The Holocene transgression is relevant to understanding the present distribution of coral reefs in the region. Flooding initiated approximately 12 kybp (=thousands of years before present) and sea level rose rapidly until

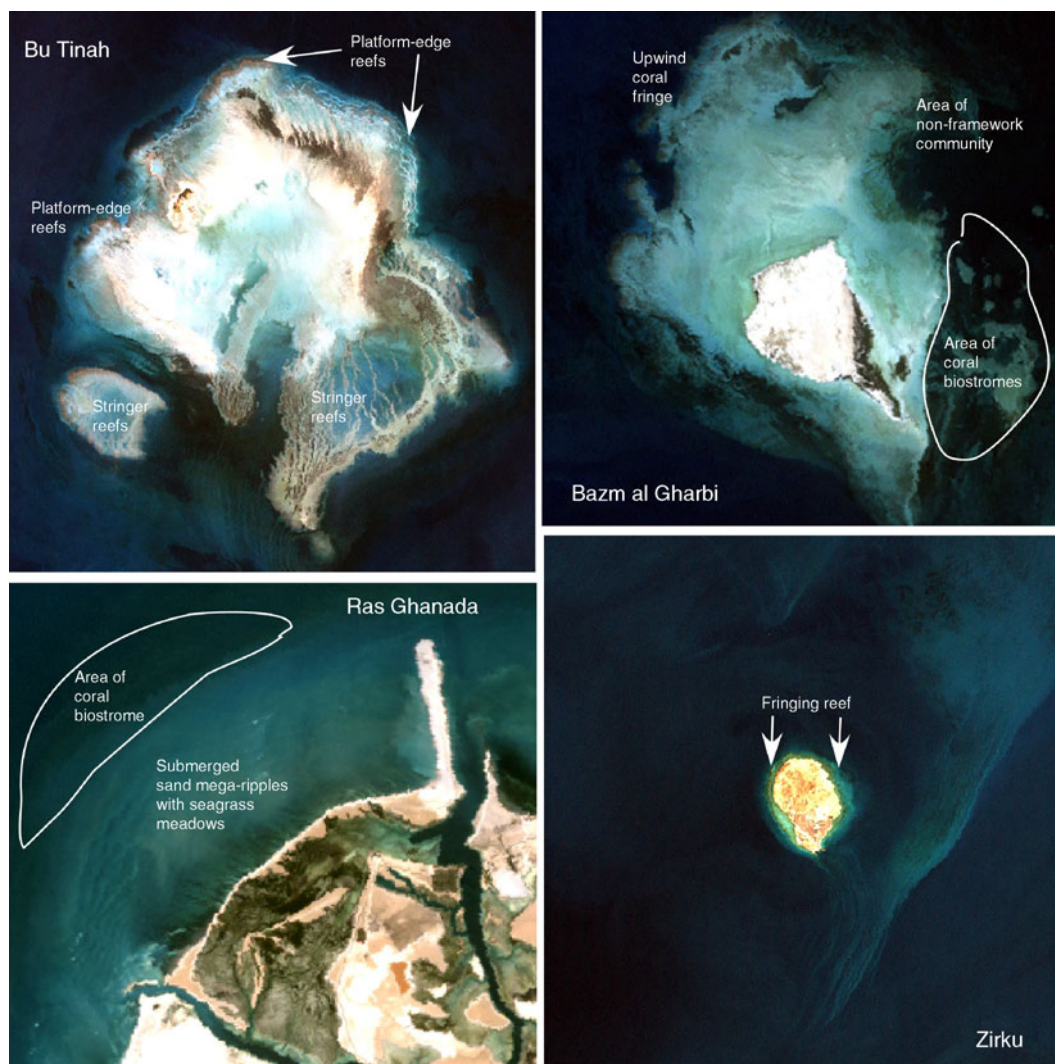
9 kybp from <90 m to <30 m below the present level. This was followed by a more gradual rise until 3–6 kybp when today's sea-level was reached. The gentle basinal slope of the Gulf, combined with a limited depth of only 90 m, made the transgression pass over parts of the shelf extremely quickly, the shoreline position routinely changing by as much as 5 km per century and certainly several orders faster as the homoclinal central shelf was inundated. Here, only an 18-m rise in elevation across a distance of about 500 km exists (Teller et al., 2000). The 4–6-m depth zone, where the majority of corals reside, has only been flooded for <4 ky and, given the lag-time required post-flooding for settlement to initiate, the modern locus of coral growth in the Gulf is relatively young.

### The coral fauna

The total Gulf scleractinian coral fauna is about 40 species (Coles, 2003) and the alcyonacean fauna is 31 species (Samimi Namin and van Ofwegen, 2009), but local diversity is usually lower. The richest local coral fauna is recorded from Saudi Arabia, around Jana and Karan islands (50 species in Basson et al. (1977), which is maybe an overestimation Vogt (1996)). The UAE coral fauna, with 34 scleractinian species, is presently the second richest known from the Gulf (Riegl, 1999). Iran should have a rich coral fauna, probably the richest in the Gulf, due to more benign oceanographic conditions. Local species richness in the Gulf is subject to temporal fluctuations



**Persian/Arabian Gulf Coral Reefs, Figure 1** Areas with extensive coral growth reported in the literature from the Gulf. Areas with confirmed coral growth are shaded gray.



**Persian/Arabian Gulf Coral Reefs, Figure 2** Reef types of the Gulf. Stringers at Bu Tinah. Biostromes surrounding banks like Bazm al Gharbi and headlands like Ras Ghanada. Fringing reefs on offshore islands (Zirku, UAE).

caused by mass mortality events that preferentially affect certain sets of species (Shinn, 1976; Riegl, 1999). A detailed study in Jebel Ali, Dubai, showed six species of *Acropora* to have disappeared regionally after the sea-surface temperature anomaly of 1996, but they later recruited into the area again (Riegl, 2002; Purkis and Riegl, 2005).

Taxonomic composition of Gulf corals is typically Indo-Pacific. Two endemic *Acropora* species (*Acropora arabensis*, Hodgson and Carpenter, 1995; *Acropora downingi* Wallace, 1999) and one endemic *Porites* (*P. harrisoni* Veron, 2000) are known. The taxonomic situation of some species (p.ex. *A. clathrata* and *A. downingi*) is not fully resolved (Wallace, 1999; Veron, 2000; Claereboudt, 2006). The closest faunistic proximity to other reefs of the Indo-Pacific is naturally to the Gulf

of Oman and then the Red Sea (Sheppard and Sheppard, 1991; Veron, 2000) due to a shared paleoceanographic history of restriction during the last sea-level lowstand and simultaneous flooding during the Holocene transgression (Sheppard and Sheppard, 1991; Uchupi et al., 1996). While the Red Sea has marked endemism (18 species), this is not the case in the Persian Gulf (three species, Hodgson and Carpenter, 1995; Wallace, 1999; Veron, 2000). The coral fauna in the southern Gulf (Peninular Arabian coast) is characterized by rarity of alcyonacean soft corals and absence of reef-building hydrozoa, which are common on other high-latitude reefs in the Red Sea and the Indian Ocean. Interestingly, soft coral cover also declines from the northern to the southern Red Sea (Sheppard et al., 1992), where conditions are similar to those in the Gulf.



## Types of frameworks

Corals occur in three biogeologic settings in the Gulf (Figure 2):

Coral reefs consisting of the in situ, interconnected framework built by the corals are small and relatively rare. The rocks of true coral reefs are solid and extend laterally over several tens to hundreds of meters and they form a clearly three-dimensional framework that rises steeply from the surrounding (usually sandy) seafloor and reaches the water surface. Such framework reefs in the Gulf can be subdivided into

- *Fringing reefs*: such as developed around most offshore islands. These classify best as incipient, or at least very young, fringing reefs in comparison with other reef areas, such as the Great Barrier Reef (Hopley et al., 2007);
- *Stringer reefs*: elongated structures, often forming a maze of several parallel and interconnecting stringers of several hundreds of meters (up to kilometers length, for example at Bu Tinah, Mubarratz);
- *Patch reefs*: small, usually round structures of sizes of meters to tens of meters. They are distinguished from

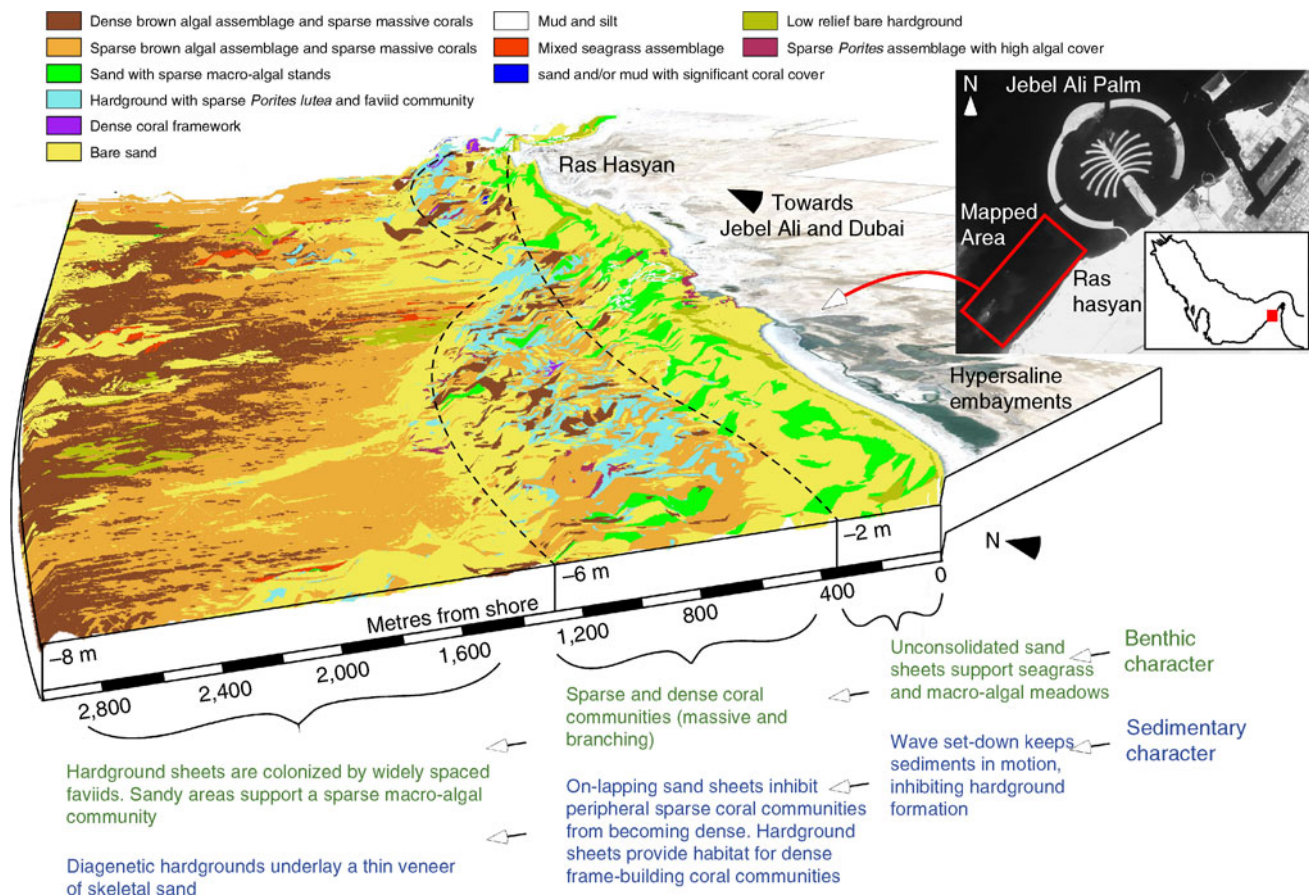
blocks of other substratum by being made up entirely by coral skeletons.

Coral carpets (or biostromes) consist of laterally thin, but continuous frameworks of coral that do not reach the water surface (Figures 2 and 3). Coral carpets are extensive and do not develop into reefs because of (1) underlying flat topography and (2) disturbance history of the local coral assemblage.

Non-framework-building coral communities are sparse assemblages of a few widely spaced corals that generally do not touch or interlock and therefore do not form a framework (i.e., coral rock). They are widely distributed throughout the Gulf (Figures 2 and 3) in any suitable habitat between about 2 and 20 m depth. Generally, biodiversity is much lower than in either coral carpet or coral reef.

## Structure of coral assemblages

The community structure of corals in the Persian/Arabian Gulf is rather uniform (Shinn 1976; Basson et al., 1977; Downing, 1985; Coles and Fadlallah, 1991; Sheppard and Sheppard, 1991; Fadlallah et al., 1995; Vogt, 1996; Riegl, 1999; Purkis and Riegl, 2005; Gischler and



**Persian/Arabian Gulf Coral Reefs, Figure 3** Near-shore habitats typical to the southern Gulf. Near-shore characterized by unconsolidated sediments supporting macro-algae and seagrass. Further offshore, sediments are not in constant motion from wave action and unconsolidated sand sheets rapidly cement to caprock, providing suitable substratum for coral communities.

Lomando, 2005). Assemblages dominated by *Acropora clathrata* or *A. downingi* have been described throughout the Gulf. These usually cap reefs or form well-defined biostromes (Figure 4). Areas of sparse *Porites lutea* or faviid growth occurs widely in sandy environments on caprock. Monospecific nodular *Porites harrisoni* (previously known as *Porites compressa*) are typical of higher temperature and salinity (43–45 ppt) stressed areas in the southern Gulf. *P. harrisoni* or faviids replace *Acropora* dominance in deeper water. During the 1996, 1998, and 2002 bleaching events, *P. harrisoni* and *P. nodifera* had markedly lower mortality than *Acropora*. Thus, these dense *Porites* assemblages may be vestiges of previous mortality events, where the *Acropora* had died and the *Porites* subsequently taken over (Riegl and Purkis, 2009).

### Environmental factors shaping coral assemblages

Responses of coral assemblages to natural stresses in the Gulf have received much attention (Downing, 1985, 1988; Coles and Fadlallah, 1991; Sheppard et al., 1992; Fadlallah et al., 1995; Riegl 1999, 2002; John and George, 2003; Purkis and Riegl, 2005; Riegl and Purkis, 2009). The differentiation of coral assemblages is most likely driven by similar factors in the entire Gulf, which has resulted in similarities in coral assemblage structure.

Differences in the substratum, like the presence of caprock and whether or not overlain by sand (and the grain size of that sand), are important for assemblage composition (Riegl, 1999; Purkis and Riegl, 2005). The Gulf is situated in a strictly arid climatic zone characterized by low rainfall and high evaporation rates (144 cm). Few perennial rivers other than the Shatt el Arab exist, and therefore continuous siltation or sedimentation from rivers is of little concern. However, most of the approximately 4–24 cm per year of rainfall occurs pulsed during the winter months with concomitant delivery of clastic sediment, particularly on the Iranian side, suppressing reef growth near river deltas or areas prone to regular flash floods with strong sediment movement. Winds shape Gulf coral reefs by stirring up sediments and mixing the water column, leading to homogeneously hot or cold conditions. Among the most notable wind patterns is the Shamal (meaning “north”), which tends to set in with great abruptness and force (Murty and El-Sabh, 1984), leading to negative storm surges that can expose shallow corals to air and decrease water temperatures below the lethal threshold for most reefal fauna. Strong local sea breeze–land breeze systems affect reefs by removing water stratification, bringing lethally heated or cooled water to reefal biota. At night, the breezes reverse, which can have a powerful desiccating effect on intertidal biota and coastal vegetation (Sheppard, 1993).

The most powerful climatic determinants of reef growth in the Gulf are temperature and salinity (Figure 5). Over 20°C temperature fluctuations between summer and winter are reported (Kinsman, 1964).

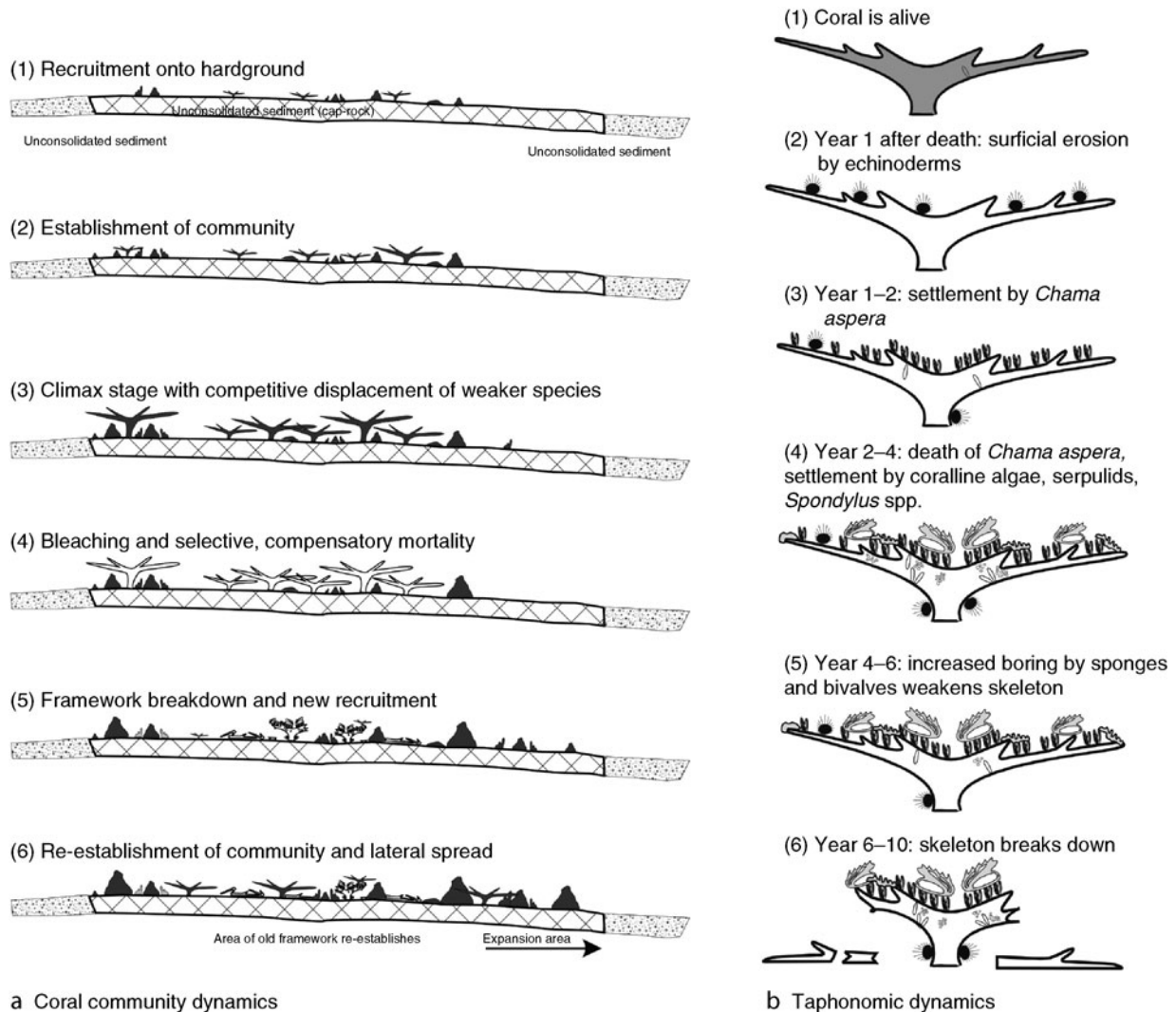
Consequently, species-specific tolerances to temperature and salinity are deciding for assemblage structure. Low tides repeatedly expose corals growing on the shallowest banks to air. Cold-related coral kills occurred in some regions in the winters of 1983, 1985, 1989, and 1992, and heat-related kills in 1996, 1998, and 2002. Temperatures can range from 37 to 14°C. Winter Shamals are often accompanied by low air temperatures chilling the seawater. In Qatar, in 1964, a Shamal chilled air temperature to 0.5°C, surface water to 4°C, and 80 km offshore at 17 m depth water temperature was 14.1°C (Shinn, 1976). Air temperatures approached the freezing point in 1982 off Kuwait, driving sea-surface temperatures to below 7°C (Downing, 1985). In the southern Gulf, fish kills are common following cold or hot weather (Sheppard et al., 1992).

Marked horizontal and vertical salinity gradients exist (Brewer and Dyrssen, 1985). Inflowing surface waters from the Arabian Sea have salinity ~36.5‰, which increases to ~40‰ along the Gulf’s E–W axis (Figure 5). Gulf waters can be differentiated into northern, less saline and southern, more saline realms. Towards the Shatt el Arab, the only continuous freshwater input, salinities decrease to ~36‰. The Gulf’s bottom waters are hyperpycnal. Highest salinities are found on the shallow Arabian side (>41.2‰), from where the deep water on the Iranian side originates (Brewer and Dyrssen, 1985; Reynolds, 1993). The Gulf of Salwah is the most saline area in the Gulf and, consequently, without reef building, and corals are rare to completely absent in its inner reaches.

### Environmental impacts and changes

Gulf coral reefs are naturally restrained by the harsh climate but are additionally increasingly subject to human impacts. Due to its extreme temperature environment, the Gulf has been presented as an ideal laboratory to evaluate coral reef persistence in global change conditions (Riegl, 2003). In the Gulf, reef corals already persist at temperatures that are forecast to affect many more temperate areas soon. Bleaching in 1996, 1998, and 2002 caused severe coral mortality in most of the southern Gulf and in 2007 in Iran (Samimi Namin, personal communication; Maghsoudlou et al., 2008; Baker et al., 2008). Recovery from such bleaching events is variable, but mortalities from nil to almost total have been reported. Stress responses of the corals are frequently species-specific, with the table corals of the genus *Acropora* affected the most during cold as well as hot events. *Acropora* table corals cover most space and build most of the carbonate structure required for reef building; therefore, such mortality has important reef-building consequences and also cause significant losses of associated biodiversity (Figure 4).

Coral predators like the crown-of-thorn starfish (*Acanthaster planci*) and the predatory snail *Drupella cornus* have not been observed in the Gulf, with exception of one specimen each of *A. planci* observed at lesser Tomb



**Persian/Arabian Gulf Coral Reefs, Figure 4** Ecological and taphonomic dynamics of coral assemblages in the Gulf: (a) Dense *Acropora* thickets with interspersed massives like *Porites* and faviids go through cycles of growth and breakdown caused by repetitive mass-mortality events due to extreme temperature (and/or salinity); (b) Breakdown of skeletons takes about 10 years, and therefore if disturbances recur within that timeframe, no lasting frameworks can be formed. This situation is common in the southern Gulf. From Purkis and Riegl (2005).

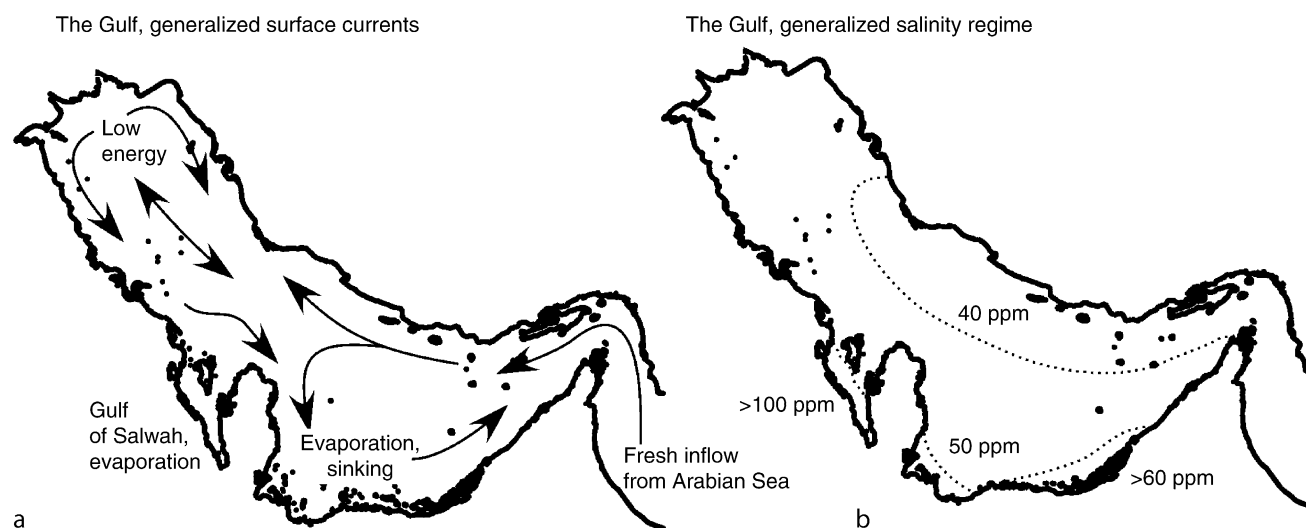
and Larak Islands (Price and Rezai, 1996). However, sea urchins occur at such high densities that the damage done to corals while grazing has raised some concern. Several coral diseases occur. Black band disease (BBD) is common on branching corals primarily during summer. White band disease (WBD) is usually rare and not infectious even in physical contact situations. Yellow band disease (YBD; Korrubel and Riegl, 1997) is the most widespread and contagious disease both in summer and winter, with fast within-colony spread (~20 mm per week in summer, 10 mm per week in winter). Neither WBD nor YBD are species-specific.

The Gulf has suffered significant loss and degradation of coral reefs and suitable coral habitats. The Arabian

Sea ecoregion (which includes the Gulf) is classified as “critically endangered” by the International Union for the Conservation of Nature (IUCN) and the World Wildlife Fund (WWF) and therefore should be the focus of priority conservation actions. The environmental plight of the Gulf was highlighted by the massive oil pollution following the first Gulf War; however, coral reefs escaped relatively unscathed (Downing and Roberts, 1993; Abuzinada and Krupp, 1994).

Overfishing is of significant concern (Subba Rao and Al-Yamani, 2000) since a lively fishing industry, locally owned but with expatriate fishermen, has sprung up over the last decades. Few of the fishing methods are sustainable, and declines of some fishstock by





**Persian/Arabian Gulf Coral Reefs, Figure 5** (a) Schematic of surface currents and circulation processes in the Gulf (from Reynolds, 1993; Lardner, 1993). (b) Overview of the major salinity trend in the Gulf (Purser, 1973).

around 80% were recorded. Significant depletion in the stocks of pelagic fishes, largely due to fisheries activities in the nursery grounds of some species, may have knock-on effects on the benthic and demersal ecosystems, such as coral reefs, which are also under ever-increasing pressure.

The gravest manmade danger to the persistence of Gulf coral reefs is their destruction due to coastal construction activities. All Gulf States have a history of large-scale dredging and reclamation of shallow marine ecosystems, like coral reefs, which would be considered prime natural assets in many countries and which are, ironically, protected by the national laws of most Gulf States. Coastal construction has led to widespread devastation particularly in the southern Gulf. Post-construction impacts such as thermal and chemical wastewater release, eutrophication, hypoxia, and hypersalinity in artificial embayments and canals, increased sedimentation, and turbidity remain long-term problems (IUCN/MEPA, 1992). Huge construction projects have in some places more than quadrupled the natural shoreline, and with little natural habitat remaining for corals, their next best option is settlement on now-abundant artificial structure, such as breakwaters, etc. They seem to have reasonable success (Burt et al., 2009) and, indeed, artificial reefs appear to be among many Gulf state's favorite construction projects. Conservation of at least some natural reefs, however, would be infinitely preferable.

## Conclusions

- The Persian/Arabian Gulf is home to dense coral communities but relatively little framework-reef building. Major framework types are biostromes, patch reefs, small fringing reefs, and stringer reefs.

- The coral fauna is depauperate but composed of typically Indo-Pacific species (about 40 scleractinia, 31 alcyonacea).
- Coral reefs in the Persian/Arabian Gulf endure the highest annual temperature variability ( $\sim 20^{\circ}\text{C}$ ) of any reef system; consequently, temperature-related mortality is a major factor influencing coral community assembly and reef building. Coral assemblages exist in a regime of repetitive mass mortality followed by regeneration.
- Other key environmental factors are salinity and substratum availability.
- Coral reef biota are under severe pressure of large-scale coastal construction throughout the Persian/Arabian Gulf, which threatens their continued existence.

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## Cross-references

Bioherms and Biostromes

Corals: Biology, Skeletal Deposition, and Reef-Building

Corals: Environmental Controls on Growth

Postglacial Transgression  
 Oil and Gas Reservoirs and Coral Reefs  
 Red Sea And Gulf Of Aqaba  
 Reticulated Reefs

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## PEYSSONNEL, JEAN-ANDRE (1694–1759)

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For 2,000 years it was believed that coral reefs were formed by stony plants (“lithophytes”), a theory which received convincing evidence in 1725 in the world’s first treatise on the “Natural History of Stony Plants” by Luigi Fernando Marsigli di Bologna (1638–1730). Under the heading *Du Corail*, Marsilius as he was known, presented a very detailed study of corals with botanical descriptions of the species examined within the appended catalogue of *Des Madreporées*.

Since their external form obviously resembles plants, Marsilius described what he believed to be calices, branches, leaves, bark, and roots, which he had studied closely with a microscope. At the time his treatise met with wide acceptance and he was invited to London to receive a Fellowship of the Royal Society and Sir Isaac Newton himself insisted on making the award.

Strenuous objections, however, were made by André Peyssonnel, a physician in Marseilles, who believed that coral reefs were not formed by plants but by “insectes” which he confirmed experimentally. Heating the water and noting that, like shellfish, they expanded and stayed out as the temperature rose; dissecting them to determine their structure and the arrangement of the eight radial petals; letting them die out of water and observing that their putrefaction gave a repulsive odor like burning animal; and finally testing them chemically with various kinds of acids to observe responses, he believed they were exactly the same as those made by other marine animals.

In 1726 Peyssonnel sent a résumé of his discoveries in the Mediterranean and Caribbean to the Paris Academy of Sciences, claiming a totally new discovery. Expansion and contraction were evidence of animal behavior, and his dissections revealed that they had exactly the same biological structure, and differed only in size and shape. He was also the first to record qualitative differences between the stem structure and function of two major groups, the soft corals with eight petals *Antipathes* and *Lithophitons*, and the stony, hard, inflexible, reef building *Madrepores* with six petals. Peyssonnel had correctly determined the animal nature of the coral-forming organism, and that reefs were limestone structures created by “insectes” living in large colonies. By 1744 he had completed his exhaustive research under the title *Traité du Corail* which was read to the Royal Society of London on 7 May 1752 and published in a short abridgment.

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## PHOSPHATIC CAY SANDSTONE

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### Definition

Phosphatic cay sandstone consists of beach materials cemented or replaced by phosphate minerals mainly in the form of dahllite (carbonate hydroxyapatite). In most instances the phosphate is derived from bird guano leached from the surface soils. It can be sufficiently concentrated for it to have been mined for agricultural fertilizer since the early nineteenth century.

### Formation

The phosphatic cay sandstone has formed entirely within the vadose zone (e.g., Stoddart and Scoffin, 1983; Baker et al., 1998), especially on relatively young islands of Holocene age. Surface soils typically 0.6 m thick (the Jemo Soils of Fosberg, 1954) are highly acidic (pH 6–4.5) and play an important role in the concentration of phosphate in what is termed the bird guano model of formation. Guano derived from bird droppings is leached downwards, but the groundwater is neutralized when it hits the alkaline calcareous cay sands beneath the humus layer and precipitation of the phosphate rock occurs.

The fresh water table beneath cays is lens-shaped, rising above mean sea level in the center of the island. The distribution of cemented deposits also has a similar morphology and may be 2–3 m thick in the center of islands but wedges out towards the beach. For example on Raine Island on the northern Great Barrier Reef (GBR) drilling has shown the phosphate not only thicker beneath the island centre but also richer in phosphate. No phosphate was found within or beneath the reef flat adjacent to or underlying the cay (Hopley et al., 2007, Figure 9.3). Coral sands have a great capacity to assimilate phosphate and the resulting sandstone may contain up to 85% phosphate as cements and bioclast replacements (Baker et al., 1998). Stalactite-like columns may be contained within the profile (see Figure 7 in entry Coral Cay Classification and Evolution), reflecting the pathways of downward-moving water in the vadose zone. Subsequent erosion of cays containing phosphatic sandstone



can produce low cliffs formed from the material, fronted by an active beach or berm.

### Relationship with *Pisonia*

There is some discussion about the relationships of phosphatic cay sandstone and stands of pure *Pisonia grandis* forest (e.g., Rodgers, 1992; Fosberg, 1994). These trees produce the necessary high acid soils and are also popular roosting sites for seabirds, the guano of which, derived from fishbones, is largely a calcium phosphate mixture. Both Rodgers and Fosberg argue that in places where *Pisonia* is not present but cemented outcrops occur, it must have been there previously and has disappeared due to natural or man-induced causes (although Fosberg also supports the idea that other species such as *Neea choriophylla* in Belize can produce similar conditions). What does appear to be necessary is a vegetation cover that produces a very acid leaf litter and soil, which react with the downward leaching guano, with *Pisonia* being the most widespread, in the Indo-Pacific.

### An alternative model of formation

Stoddart and Scoffin (1983) described phosphatic sandstone of various kinds, especially the contrasts between the deposits of relatively young (Holocene) cays and those of high islands such as the uplifted atolls of Makatea and Nauru. Rodgers (1992) acknowledged such differences between high and low islands and identified small variations within single deposits, and applying a variety of terms to deposits with only small differences. Fosberg (1994) had used a simple term “atoll phosphate rock” to cover all these nomenclatures.

However, the bird guano model of phosphate accumulation does not seem applicable to the large deposits of high islands and has been rejected for quantitative and qualitative geochemical reasons (Rougerie et al., 1997). Ponds within enclosed or uplifted lagoons are nutrient rich and accumulate mats or “kopara,” rich in chlorophyll and carotenoid pigments. Whole areas of brackish lagoons may be covered by such mats and accumulate to thicknesses of 1–6 m. Partial desiccation results in thick layers of fluorapatite with the potential to produce millions of tons of ore with 30% phosphorous content, clearly an accumulation with which the bird guano model cannot compete.

### Mineralogy

Analyses of phosphate rock from around the world are very similar with dahllite (carbonate hydroxyapatite) being the main mineral in micro laminated grain coatings and bioclast replacement (e.g., Stoddart and Scoffin, 1983; Baker et al., 1998). However, tricalcium phosphate may also appear in the cements, which have a concentration of only 5–8% while the bioclastic replacement values can be as high as 85%. Stoddart and Scoffin (1983) also suggest that pre-Holocene phosphatic sandstones may contain francolite (carbonate fluorapatite) as the fluorine content of insular phosphate gradually increases with time.

### Age and rate of accumulation

The age of phosphate rocks on some high islands may be pre-Quaternary. For example, a Pliocene age has been established for the phosphorite on Navassa Island, just west of Haiti (Miller et al., 2008). However, bird guano deposits occur mainly on young islands of Holocene age. For example, on Raine Island (GBR) the reef flat underlying the deposits has been dated at 4,780 years B.P. while clam shells from within the deposit suggest that phosphatization has occurred in the past 1,200 years only (Baker et al., 1998). Similar ages come from phosphate deposits on Lady Elliott Island at the southern end of the GBR, where reef flat construction dates from 6,500 years B.P. and phosphatization since 3,200 years B.P. (Chivas et al., 1986). Rodgers (1992) notes that phosphatization has occurred in Sakula either as a continuous or episodic process within the vadose zone for at least 4,000 years, that is, for as long as the island has existed.

Few data are available for rates of accumulation, although Chen and Krol (1997) examining nutrient dynamics at Heron Island on the southern GBR produced some relevant estimates. Guano deposition varies seasonally with 164,000 shearwaters (*Puffinus pacificus*) and white cap noddies (*Anous minutus*) depositing nearly 5,000 kg of guano a week over the 19 ha cay during 1992. The guano contains 7.3% N and 1.5% P by weight and thus delivers to the cay surface about 9,800 kg N and 2,000 P annually. The potential for accumulation of phosphatic cay sandstone over the 6,000 or so years of island existence is significant. However, no phosphatic sandstone has formed on this island (see below).

### Phosphatic deposits and eutrophication

The Heron Island study by Chen and Krol (1997) mentioned above aimed at determining the nutrient loading of the islands groundwater both naturally by leached guano and by anthropogenic contaminants. Tidal phenomena dominate the groundwater hydrodynamics and because the groundwater is nutrient rich it has the potential to influence ambient N and P levels in its adjacent reef environment. However, the phosphorous derived from the guano remains on the surface as a thin layer. In the coral cay environment, dissolved inorganic P is absorbed by aragonite and calcite. The coral sediments of the unsaturated zone act as a filter between the P-PO<sub>4</sub> of the groundwater and the adjacent reef flat waters. Chen and Krol (1997) also noted that tidal flushing and the capacity of the reef to assimilate additional nutrients are also factors in limiting the potential for “natural eutrophication” though further research is needed.

### Utilization of phosphatic cay sandstone and resulting environmental impacts

Although phosphatic cay sandstone has varying degrees of cementation, it has a natural significance very similar to beach rock. It can help “armor” the beach face, retard



**Phosphatic Cay Sandstone, Figure 1** The light tower on Raine Island, northern GBR, Australia, built of phosphate rock by convict labor in 1844. In the foreground is the low phosphate cliff (ca 0.5 m) formed by erosion at this end of the island.

erosion by forming low cliffs, and provide anchor points for reorientation of cay beaches.

It has also had wide anthropogenic uses (e.g., Stoddart et al., 1981). Where sufficiently hardened, it has been used as a building stone, one of the most historic sites being the earliest navigational beacon on the GBR built on Raine Island in 1844 by convict labor. It still stands though has required repairs on a number of occasions, (Figure 1).

More widespread is the use of phosphatic cay sandstone as an agricultural fertilizer. This was particularly so in the nineteenth century when thousands of tons were removed from reef islands around the world. This was a particularly profitable industry where phosphate concentrations approached their maximum of about 80%. At most locations the thickest (>2 m) and richest (>50%) occurred in the centre of the islands. Vegetation was cleared, temporary buildings constructed, and even tramways and wharfs built on the most remote of islands.

Environmental impacts were devastating and in some locations recovery has still not taken place (Hopley, 1988, 1989; Daley and Griggs, 2006). *Pisonia* forest has rarely returned but weeds, introduced during the period of exploitation, may now be a permanent feature of the flora. In fact, guano mining is probably the most lasting of all the anthropogenic impacts on GBR islands, having taken place on nine reef islands and one high island (Holbourne), which has an area of Holocene carbonate sediments, similar to the older cays including three



**Phosphatic Cay Sandstone, Figure 2** The central guano flat on Raine Island still largely bare of vegetation 100 years after the end of phosphate mining. The central flat originally had a guano deposit about 1.5 m thick, overlain by a black soil.

phosphatized beach ridge terraces (Hopley, 1975), which were mined between 1918 and 1921 (Daley and Griggs, 2006). The degraded quarry remains as a reminder of the impact of mining on the physical environment. However, on Raine Island and elsewhere on the GBR, the small decline in seabird roosting and nesting appears to be more recent than the time of phosphate mining (1890–1892). Batianoff and Cornelius (2005) relate this to climatic and oceanographic changes in surrounding waters rather than devastation caused by the mining (Figure 2). Sixteen species of birds (some uncommon or rare) still nest on Raine Island, which is also the most important nesting site of the green turtle *Chelonia mydas* in the world (Limpus et al., 2003).

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## Cross-references

Beach Rock  
 Coral Cay Classification and Evolution  
 Coral Cays-Geohydrology  
 Makatea  
 Mining/Quarrying of Coral Reefs  
 Nutrient Pollution/Eutrophication  
 Palaeosols  
 Soils of Low Elevation Coral Structures

## PLATE TECTONICS

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## Synonyms

Continental drift

## Definition

*Absolute plate motions* (APM): Motion of tectonic plates relative to a fixed point in the mantle, typically defined by one or more hot spots (i.e., the hotspot reference frame).

*Apparent polar wander* (APW): Motion of the north pole as seen from a moving tectonic plate.

*Relative plate motions* (RPM): Motion of tectonic plates relative to each other, typically inferred from marine magnetic anomalies and the geomagnetic timescale.

*True polar wander* (TPW): Rotation of the entire solid Earth leading to a realignment of the rotation (and geomagnetic) axis.

## Introduction

Reefs build on shallow-water geologic foundations (e.g., continental shelves, tectonically active oceanic islands) that slowly undergo horizontal (due to plate tectonics) and vertical (thermal and flexural subsidence) movements over time. As plates move laterally, coral-rich areas may move to latitudes where coral growth is inhibited (e.g., Grigg and Epp, 1989). Furthermore, long-term plate tectonic changes in the configuration of landmasses can alter the global oceanic circulation, thus affecting the colonization of coral (e.g., Grigg, 1997). Understanding absolute plate motions is thus important for understanding long-term coral variability and the history of global biodiversity patterns (e.g., Renema et al., 2008). The main purpose of this article is therefore to



give an overview of absolute plate motions, the assumptions used, and the current status of plate tectonic research.

Plate tectonics, the major paradigm for how the Earth works, was established in the 1960s following decades of observational research that culminated in the key discoveries of geomagnetic reversals, mid-ocean ridges, transform faults, and seafloor spreading. Collectively, these insights gave rise to the “new global tectonics” or theory of plate tectonics (e.g., Wessel and Müller, 2007). The history of RPM is inferred from the mapping of marine magnetic anomalies and seafloor morphology using implementations of Euler’s theorem for rotations on a sphere. Using improved observations of seafloor morphology derived from multibeam bathymetry and satellite gravity, combined with better coverage of magnetic anomalies, has allowed researchers to improve the resolution of RPM models. The global crustal age models derived from a worldwide compilation of RPM studies (Müller et al., 2008) perhaps best represent the state of the art (Figure 1). However, RPMs do not let scientists examine changes in latitude, and thus an absolute reference frame is needed. APMs typically refer to motion relative to a fixed mantle, and the most prominent mantle reference that has been proposed is the “fixed hotspot” reference frame.

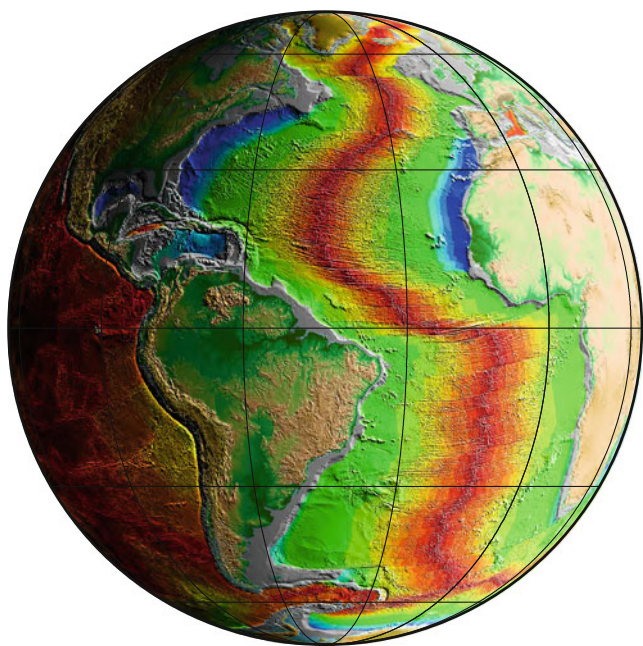
The hotspot reference frame is derived from the geometries of dated hotspot islands and seamount chains

(e.g., Duncan and Clague, 1985) and was introduced by the plate tectonics pioneers Wilson (1963) and Morgan (1971). The foundation of this absolute reference frame, that is, the fixed hot spots, has been the focus of much research during the last few years (e.g., Koppers et al., 2001; Steinberger and Torsvik, 2008; Wessel and Kroenke, 2008). The Hawaii-Emperor chain and its famous bend have been interpreted as the prime surface manifestations of the changing Pacific plate motions over a stationary mantle plume; in fact, this interpretation has reached textbook status. However, over the last decade, a more complicated picture has emerged. Paleolatitudes of the Emperor seamount chain have been inferred from the frozen-in paleomagnetic field, and these imply a birthplace significantly farther north than the present location of the Hawaiian hot spot. The most logical conclusion is that the Hawaiian plume must have been further north in the past and subsequently drifted south (Tarduno et al., 2003). The extent to which such drift contributed to the prominent Hawaii-Emperor bend, now believed to have formed ~47–50 Ma (Chron 21–22), is the topic of ongoing research and has the potential to significantly revise established models of APMs.

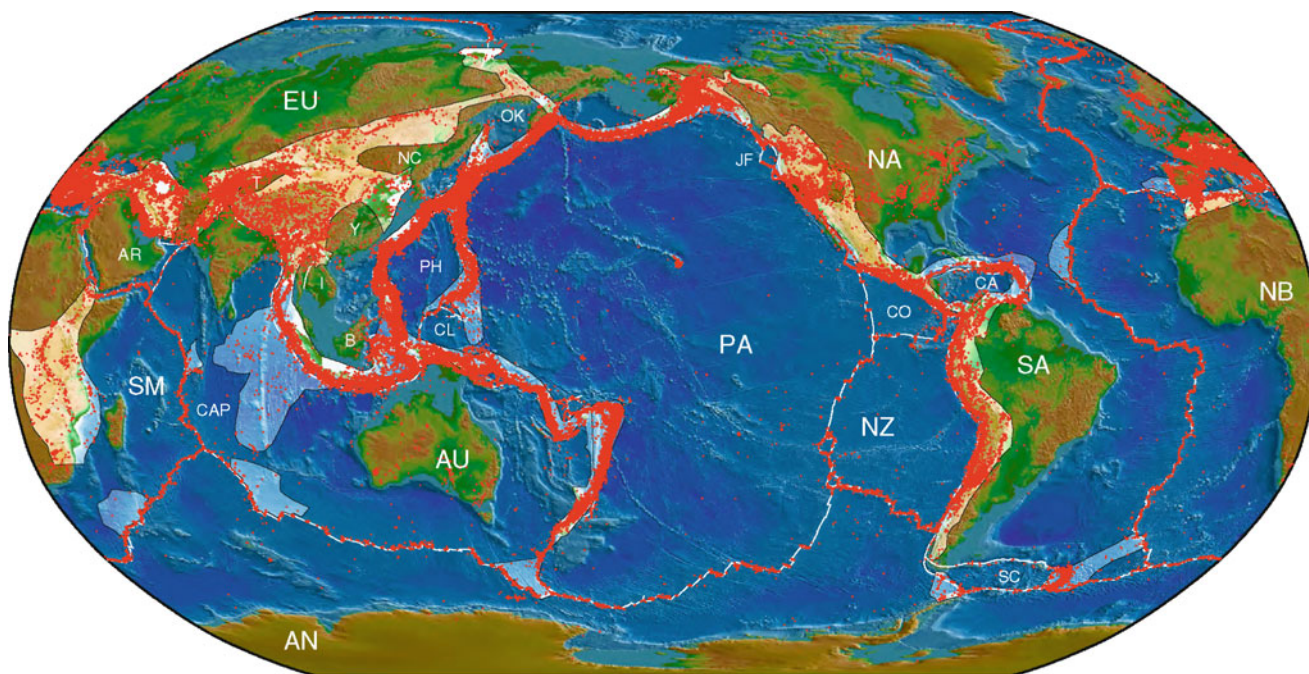
### Plate tectonics

Seafloor spreading, a key component of plate tectonics, was developed in the early 1960s (Dietz, 1961; Hess, 1962) when it was first realized that new seafloor is created at mid-ocean ridges, spreads away from them as it ages, and is recycled at subduction zones. However, earlier and remarkably similar ideas had been suggested by Holmes (1944). A key insight came from Wilson (1965), who introduced the concepts of plates and transform faults. Wilson argued that the Earth’s active mobile belts were continuous, marked by active seismicity, and divided the Earth into a set of approximately a dozen rigid plates. These active mobile belts consist of ridges where plates are created, trenches where plates are destroyed, and transform faults that link the other two belts.

Plate tectonics theory states that the Earth’s surface is an interlocking, internally rigid set of plates in constant relative motion. Plates are rigid except at their boundaries, which are weak lines between contiguous plates. Earthquakes occur due to the relative motion between plates; in fact, the earthquakes define the plate boundaries (Figure 2). Three types of plate boundaries are recognized: (1) divergent boundaries – where new crust is produced, (2) convergent boundaries – where crust is recycled as one plate subducts beneath another, and (3) transform boundaries – where crust is preserved as two plates slide horizontally past each other. Complications can arise in some areas. For instance, in places where the boundaries are not well defined, the deformation tends to extend over a broad plate-boundary zone (Gordon, 2000). Such plate-boundary zones tend to have complex geology and deformation, possibly involving one or more microplates.



**Plate Tectonics, Figure 1** Relative motion between plates as evidenced by marine magnetic anomalies. Combined with a geomagnetic reversal timescale, one can create crustal age grids (Müller et al., 2008). The relative motions between plates are very well determined, but it is the absolute motions of plates relative to a fixed point in the mantle that let us examine any changes in latitude that may affect reef colonization.



**Plate Tectonics, Figure 2** Map showing idealized narrow plate boundaries (white lines, Coffin et al., 1997), shallow (0–70 km depth) seismicity (red dots, Engdahl et al., 1998), and regions of diffuse plate boundaries (areas of lighter illumination, Gordon, 2000). Plate abbreviations: B Borneo, AN Antarctica, AR Arabia, AU Australia, CA Caribbean, CAP Capricorn, CL Caroline, CO Cocos, EU Eurasia, I Indo-China, JF Juan de Fuca, NA North America, NB Nubia, NC North China, NZ Nazca, OK Okhotsk, PA Pacific, SA South America, SC Scotia Sea, SM Somalia, Y Yangtze, T Tarim Basin, PH Philippine.

### The morphology of the ocean floor

Wilson (1963) realized that some regions, such as Hawaii, have been sites of long-term volcanic activity. Such focused volcanism would seem to imply that relatively small, stable, and anomalously hot regions (hot spots) exist beneath the plates, supplying high heat energy (i.e., a thermal plume) to maintain the surface volcanism. Wilson suggested that the alignment of the Hawaiian Islands-Emperor seamounts chain must have resulted from the Pacific plate passing over a fixed hot spot deep in the mantle, now located beneath the Island of Hawaii. Morgan (1971) further elaborated on this idea and developed the fixed hotspot hypothesis. About 100 hot spots have been proposed to be active during the past 10 million years (e.g., Burke and Wilson, 1976). The majority are located beneath plate interiors (e.g., the African plate), but others can be found near a mid-oceanic ridge system, such as the hot spot beneath Iceland, the Azores, and the Galapagos Islands. The standard way of reconstructing plates relative to a fixed mantle relies on linear chains of volcanoes that exhibit a monotonic age progression and can be traced back to singular spots of melting in the upper mantle (see *Oceanic Hotspots*). Mapping seamounts thus became an important prerequisite to deciphering APMs.

Even prior to Wilson's realization, it was well known that the seafloor was littered with underwater volcanoes

known as seamounts. During the war, Hess (1946) found and mapped several flat-topped seamounts that he named guyots; these seemed to be former islands that had been worn down to sea level and eventually had drowned. After World War II, a flurry of ocean-going expeditions equipped with echo-sounding instruments heralded major advances in the mapping of seafloor morphology, including the discovery that the oceans possessed mountain chains of extraordinary lengths. These facts were popularized by the famous physiographic maps of Lamont's Heezen and Tharp (1961, 1964), rendering ubiquitous abyssal hills and majestic seamounts. Surveys of seamounts in the Pacific suggested that there might be as many as 100,000 seamounts exceeding a height of 1 km in the Pacific alone (Menard, 1964). Nevertheless, given the vastness of the oceans and the sparse sampling provided by surface ships, the large majority of seamounts were never charted. Statistical analyses of seamount populations were limited to extrapolations from smaller, well-surveyed areas by dense, single-beam echo-sounding tracks or by the improved coverage of the newer multi-beam systems in the early 1980s (e.g., Smith and Jordan, 1988).

Space-age technology brought satellite altimetry as a new technique for the study of oceanography and, indirectly, seamounts. The global gravity maps developed from Seasat altimeter data portrayed a previously unseen

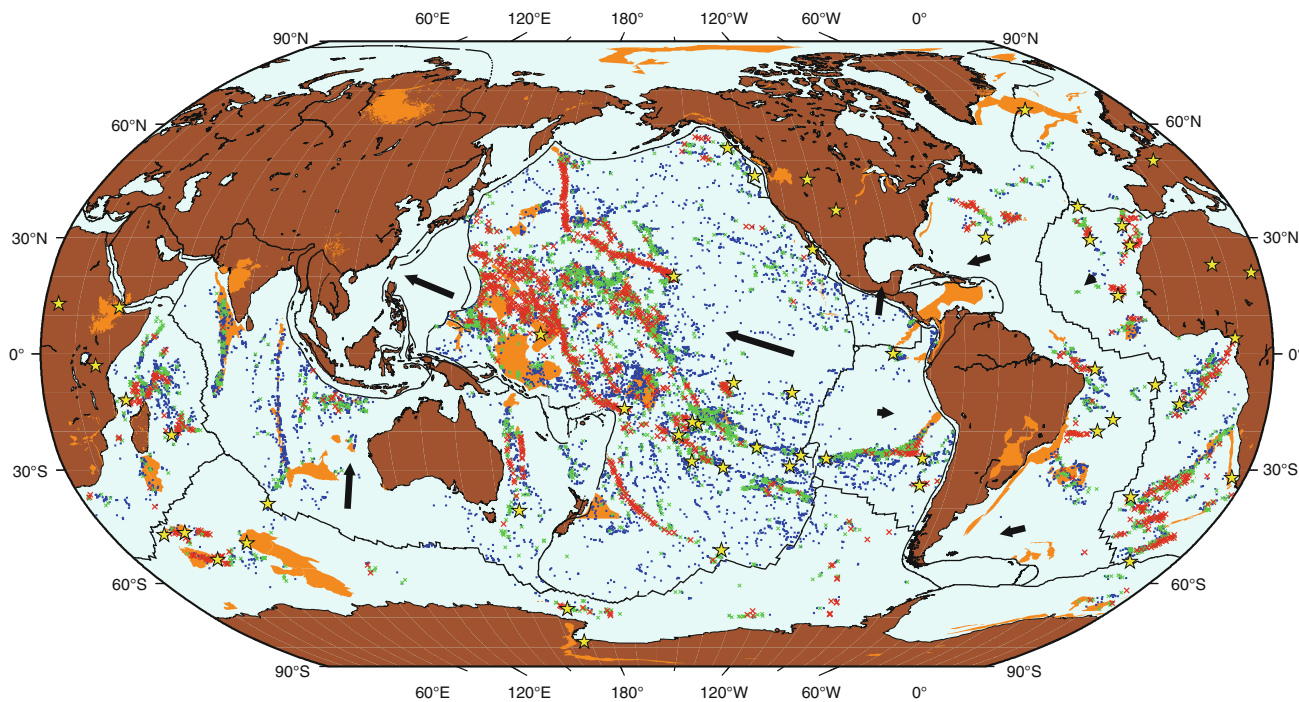


level of detail of seafloor fabric, including numerous underwater volcanoes (Haxby, 1987; Haxby et al., 1983). Using along-track profiles of sea surface heights from the Seasat mission, Craig and Sandwell (1988) pioneered a global investigation into the distribution of seamounts, discovering ~8,500 individual edifices throughout the world's oceans. Key findings were that the Pacific Ocean basin contains most of the seamounts and that in particular the Western Pacific displays an unusual high density of large seamounts. Unfortunately, the large track spacing (~100 km) meant that many seamounts were only partially surveyed and still more were left undiscovered in the gaps between tracks. The later Geosat/ERS-1 altimetry missions greatly improved the coverage by having closer track spacing (a few kilometers) and resulted in much improved global gravity grids (Sandwell and Smith, 1997). Using such grids, Wessel and Lyons (1997) characterized ~8,900 seamounts in the Pacific Ocean alone, with the majority of them being smaller, hitherto uncharted seamounts. Wessel (2001) expanded the analysis globally, finding almost 14,700 seamounts, now adjusted down to 11,800 due to duplicates (Wessel et al., 2010). The size-frequency distribution suggests that sizes of seamounts appears to follow a power-law relationship, which can be extrapolated to match Menard's original prediction of ~100,000 seamounts of at least 1 km in height (Figure 3). Scientists

now routinely study even smaller seamounts (e.g., 50–100 m tall), and should the inferred frequency-size relationship hold for such small seamounts one would predict a global population into the millions. If valid, this would make these morphological features second in ubiquity only to the abyssal hills (e.g., Macdonald et al., 1996).

### The ages of seamounts and oceanic islands

The geometries of seamount chains place strong constraint on plate motions. However, the hotspot hypothesis predicts there should be a monotonic age progression along seamount and island chains formed by hotspot volcanism. Hence, determining the ages from rock samples collected at these sites became another key undertaking. Dredging of seamount flanks and sampling from oceanic islands built up a valuable data set whose importance cannot be overstated (Duncan, 1981; Duncan et al., 1985; McDougall, 1971; Turner and Jarrard, 1982; Turner et al., 1980). Recently, Clouard and Bonneville (2005) reviewed a compilation of more than 1,500 individual age-determinations from ~300 different Pacific volcanoes. The available data seem to suggest that monotonic age progressions are indeed observed along several of the Pacific island and seamount chains, but for others the pattern is less clear (e.g., Dickinson, 1998; McNutt et al., 1997). The key difficulty in assessing age-progressive



**Plate Tectonics, Figure 3** Distribution of seamounts inferred by satellite altimetry (Wessel, 2001). Colors reflect estimated seamount sizes (blue are ~1–2 km, green are 1.5–4 km, and red are >3.5 km tall). Most seamounts are found in the Pacific basin, with significant populations in both the Atlantic and Indian oceans. Hot spots (yellow stars) are often found near the young end of chains. Large igneous provinces (LIPs; orange) are often associated with seamount provinces. Black arrows indicate current absolute plate motions (for scale, the Pacific plate arrow length represents a velocity of 10.8 cm/year).



volcanism is the lack of available samples. Furthermore, as the field of radiochronology has advanced, there is a great need to reanalyze older samples. Finally, the discovery that volcanism at a given site can remain active over an extended period (e.g., Pringle et al., 1991) makes it problematic to determine if the observed age represents the feature as a whole. For instance, in some areas where new samples have been obtained and the latest dating techniques have been applied, significant discrepancies between the new and old dates were found (e.g., Koppers et al., 2004). While such reanalysis is necessary, one must be careful when combining old and new ages in age-progression studies. Surprisingly, some Pacific chains that have geometries similar to the Hawaii-Emperor bend have recently been dated, yielding ages that are incompatible with a hotspot origin (Koppers and Staudigel, 2005). Perhaps the volcanism was instead triggered by transient stresses during times of plate motion changes, leading to decompressional melting that rises up through preexisting zones of weakness (e.g., Sager and Keating, 1984; Wessel and Kroenke, 2007). Such complications continue to make studies of age-progressive volcanism challenging.

Outside the Pacific, the situation is similar: Apparent age progressions are often found for long seamounts chains, but unfortunately both the quality and quantity of samples are much lower than for the Pacific (e.g., Baksi, 1999). It is clear that recent advances in dating techniques promise to raise the quality of radiometrically determined ages to a higher level (e.g., Koppers et al., 2004). However, this will take time, as reanalysis is a time-consuming and costly endeavor. Furthermore, the acquisition of new samples, in particular for older chains, is also a difficult and expensive undertaking and may ultimately require ocean drilling for reliable results (Tarduno et al., 2003). Therefore, the study of APMs is a topic constantly in need of more and better data.

### Studies of absolute plate motions

In recent decades, our understanding of the Mesozoic and Cenozoic RPM between the major tectonic plates has improved considerably, even though APM relative to a “fixed” underlying mantle is still controversial. Marine magnetic anomalies, some as old as 165 million years, along with fossil seafloor fabric based on bathymetry and altimetry clearly constrain RPMs for most of the major plates (Müller et al., 2008). Paleomagnetic data and hotspot traces are among the concepts that have been used to attempt to constrain APM. Paleomagnetic data may provide the paleo-meridian orientation and paleolatitude of a plate; together these determine the paleopole for a given plate. However, because the Earth’s dipole field is axisymmetric, no paleo-longitudinal information is obtained from paleomagnetic data. Hotspot tracks with linear age progressions can be used to restore plates to their original positions by assuming that hot spots are approximately fixed relative to each other (i.e., the “fixed hotspot hypothesis”). However, an early indication

of problems to come appeared when Molnar and Stock (1987) showed that during the Tertiary, the Hawaiian hot spot apparently had moved at 10–20 mm/year relative to the Iceland hot spot and to hot spots beneath the African and Indian plates. Recently, new analyses have questioned the magnitude and significance of this conclusion (Andrews et al., 2006).

Numerous paleomagnetic data sets and models for the APM of the North American, African, and Eurasian plates during the Mesozoic and Cenozoic have been published (e.g., Engebretson et al., 1985). Unfortunately, there are inconsistencies between different apparent polar wander paths and hotspot models. Especially for times prior to 47 Ma, large misfits are found between APM models based on hotspot tracks and those based on apparent polar wander paths from paleomagnetic data (e.g., Sager, 2007). The key plates whose APM forms the basis for our global understanding are the African and Pacific plates.

### Motion of the African plate

Assuming fixed hot spots, Müller et al. (1993) proposed a key African APM model based on a refined model for global RPMs, bathymetry, and radiometric age dates of major hotspot tracks. They combined the major hotspot tracks with observed age progressions from the Atlantic and Indian oceans and employed an interactive technique to derive a “best-fit” qualitative model for motions of the major plates in the Atlantic-Indian domain relative to those hotspot tracks that had clear age progression.

Despite the popularity of this model, it had some well-recognized limitations. The Late Tertiary portion of this model was largely unconstrained by radiometric ages, based on the lack of published age dates. Before 80 Ma, the only hotspot tracks with age progression in the Atlantic-Indian oceans are the New England seamount chain (tied to the Great Meteor hot spot on the Africa plate) and the Walvis Ridge/Rio Grande Rise (likewise linked to the Tristan da Cunha hot spot) in the Atlantic Ocean (Duncan, 1984; O’Connor and Duncan, 1990). Consequently, the APM of the Indian, Australian, and Antarctic plates must be computed by plate circuit closure for these times. When the Müller et al. (1993) model was constructed, pre-80 Ma RPMs in the Indian Ocean were poorly known, due to a lack of data in crucial areas, especially offshore Antarctica in the Enderby Basin and areas south of the Kerguelen Plateau. There, a sequence of Mesozoic magnetic anomalies was subsequently mapped and modeled, originating at ~130 Ma (Gaina et al., 2007; Gaina et al., 2003). However, the Müller et al. (1993) model (incorrectly) assumed a post-120 Ma breakup between India and Madagascar. Disagreements between hot spot and published paleomagnetic reference frames have surfaced for India (Müller et al., 1994) and Australia (Idnurm, 1985), suggesting that the mantle beneath the Indian Ocean cannot be considered a fixed reference frame. This mismatch directly affects estimates of latitude. For instance, paleopoles for India from the

Rajmahal Traps (Das et al., 1996; Rao and Rao, 1996) result in a 47°S paleolatitude of the traps at their time of formation (~117 Ma) (Baksi, 1995), whereas the Müller et al. (1993) model places them at about 40°S; both estimates have an uncertainty of  $\pm 400$  km.

Comparing mid-Cretaceous (122–80 Ma) paleolatitudes of North America and Africa with estimates from hotspot tracks (Van Fossen and Kent, 1992) indicates an 11–13° misfit. This discrepancy suggests that Atlantic hot spots were not fixed relative to the Earth's spin axis before 80 Ma, but moved southwards by as much as 18° (Torsvik et al., 2002) during 130–100 Ma. Others have argued that this apparent southward movement was caused by true polar wander (TPW) (Prevot et al., 2002), but this has been refuted by Tarduno and Smirnov (2002).

The Müller et al. (1993) APM model predicts a relatively sharp bend of plate motion directions (e.g., of Australia and Antarctica) at about 80 Ma. This property originates from the bend between the New England seamount chain and the Corner seamounts at roughly 80 Ma in the central North Atlantic. An equivalent bend in fracture zones is not found in either the Atlantic or Indian Oceans. Revisiting the Africa APM, O'Neill et al. (2005) allowed for moving hot spots in order to satisfy both paleomagnetic constraints and hotspot chain geometry and age progression. They found evidence for plume motion on the order of 5–10° prior to 80 Ma; however since that period any plume motion is less than the model uncertainties. These improvements place India farther north in the past than what conventional fixed hotspot models do.

### Motion of the Pacific plate

The Hawaiian chain is clearly the most studied hotspot chain and has as its most characteristic feature the prominent bend near longitude 172°E, here called the Hawaii-Emperor Bend (HEB; see *Oceanic Hotspots*). Since Wilson (1963) first suggested it, the HEB has been explained by a ~60° change in direction of Pacific plate motion over a stationary hot spot in the mantle (Morgan, 1971). In fact, the geometries of the Hawaii-Emperor chain and many coeval chains (Figure 4) have been used to model the Pacific APM (e.g., Duncan and Clague, 1985; Koppers et al., 2001; Wessel et al., 2006; Wessel and Kroenke, 2008; Yan and Kroenke, 1993). A puzzle, however, was represented by the age of the bend, initially dated to 43 Ma (Dalrymple et al., 1987). Scientists expected that such a large reorientation of the motion of the dominant Pacific plate should have left abundant evidence of contemporaneous tectonic and magmatic events along the plate boundary; however, careful assessments of the geologic record failed to uncover such evidence (Atwater, 1989; Norton, 1995). Furthermore, rock samples obtained from drilling the Emperor seamounts revealed a frozen-in paleomagnetic field best explained if the seamounts had formed significantly further north (5–10°) of the present-day location of Hawaii (Kono,

1980; Tarduno and Cottrell, 1997). Subsequent efforts to project the APM of Africa, via the global plate circuit, into the Pacific failed to reproduce the shape of the HEB (Cande et al., 1995; Raymond et al., 2000). These inconsistencies lead to alternative models where the plume sustaining the volcanism was no longer stationary (Steinberger, 2000; Steinberger and O'Connell, 1998). Such models could fit both the changing latitude of the hot spot (as suggested by paleomagnetism) and the geometry and age progression of the seamount chain. Some researchers concluded that no change in Pacific APM had taken place at all: Since the trail records the vector sum of plate and plume motion, it could be reconstructed by a rapid slowdown in the southward motion of the plume while Pacific plate motion remained unchanged in direction and magnitude (Tarduno et al., 2003).

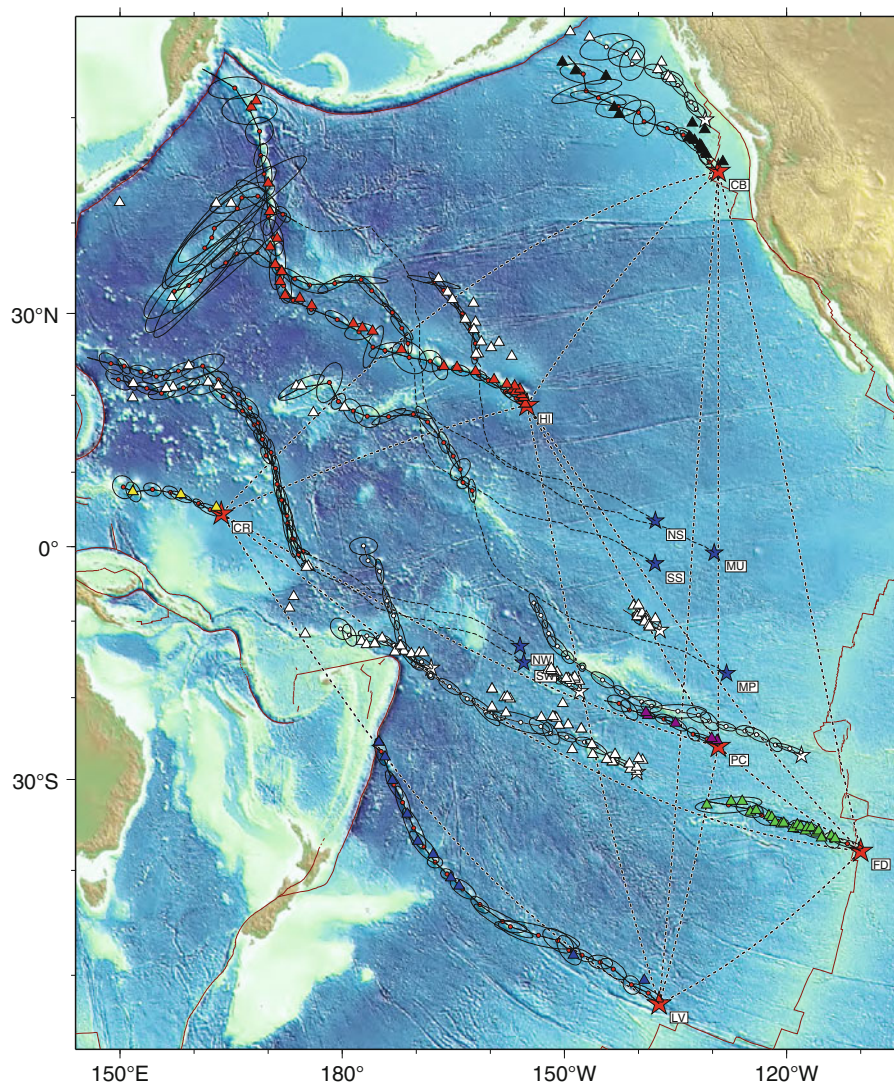
To reconcile APM models inferred from the Indian, Atlantic, and the Pacific oceans requires their propagation via the global plate circuit (Acton and Gordon, 1994). Because the history of all RPM changes between conjugate plate pairs is not known, the projection of the African APM into the Pacific is subject to uncertainties that cannot easily be quantified. For instance, by choosing a different plate circuit for connecting the Pacific to Australia via the Lord Howe Rise, Steinberger et al. (2004) showed that the HEB did seem to require a plate motion component and thus could not only be caused by plume drift alone. Meanwhile, a reanalysis of the rock samples taken from around the HEB region revealed that the HEB is apparently much older than originally determined. Sharp and Clague (2006) found that the rocks around the bend erupted during the 47–49 Ma interval (Chron 21–22) and, by allowing for 1–2 million year construction time, that the bend itself could have formed even as early as 50 Ma – fully 7 million year earlier than previous estimates. This older age complicates many of the previous conclusions about the lack of correlation between the HEB and plate boundary processes, since Chron 21–22 is generally recognized as an active tectonic period in the Pacific and elsewhere (Cande et al., 1995; Rona and Richardson, 1978). Sharp and Clague (2006) examined details of the age progression and concluded it was unlikely that the plume was moving during the formation of the bend, thus favoring the original explanation (purely a plate motion change over a stationary hot spot) for the origin of the HEB.

### Discussion

APM studies continue to be carried out in the aftermath of these discoveries. For instance, Whittaker et al. (2007) presented new tectonic evidence for a change in plate motion between Australia and Antarctica; this kink appears to coincide in time with the HEB. This change in plate motions may further affect the global plate circuit and results that are derived from its use.

Recently, the case for moving hot spots was reviewed by Tarduno et al. (2009). They argued that mantle-scale flow models could explain the types of plume drift



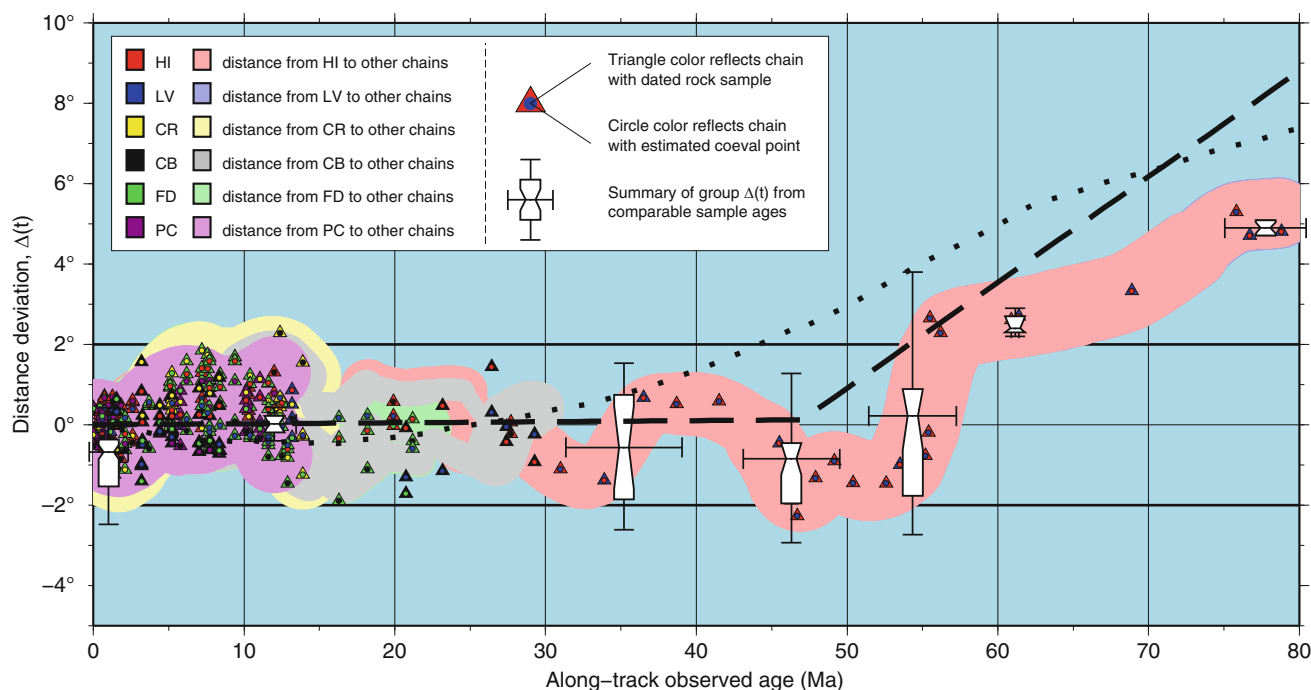


**Plate Tectonics, Figure 4** Map of the Pacific hemisphere with location of dated rock samples (*triangles*) from the Hawaii-Emperor (HI; *red*), Louisville (LV; *blue*), Foundation (FD; *green*), Pitcairn (PC; *magenta*), Caroline (CR; *yellow*), Cobb (CB; *black*), and other Pacific seamount chains (*white*). *Red (blue) stars* represent presently active (extinct) hotspot locations, while solid lines represent the WK08-G APM model geometry (Wessel and Kroenke, 2008); ellipses indicate 95% confidence regions. *White stars* represent active hotspot locations for chains not used to constrain the APM model. *Heavy dashed lines* represent the 15 inter-hotspot separations between the six chains identified. *Dark red lines* are plate boundaries (redrawn from Wessel and Kroenke, 2009).

inferred from the Hawaiian plume by the observed paleolatitudes from the Emperor seamount chain. In fact, they suggested that hotspot tracks, rather than constraining the APM, may instead give insight into the patterns of past mantle convection. At the same time, the distances between same-age samples in the Hawaii-Emperor and Louisville chains were analyzed, suggesting relatively minor changes in the separation of these two hotspots through time (Wessel and Kroenke, 2009). In the critical time period 80–47 Ma, this separation decreased by perhaps 3–5° (Figure 5), compared to 7–9° predicted by moving hotspot models (Koppers et al., 2004; Steinberger and Gaina, 2007). There appears to be several ways

to satisfy both the quantified distance constraints and the observed paleolatitudes: (a) if the Hawaii plume was farther north at 90 Ma but moving southward (to satisfy the paleolatitudes), then the Louisville plume must have been much farther north as well (to match the observed hotspot separations). Given the variability in modeling results of the Louisville plume motion (e.g., Antretter et al., 2004), it is possible that a combination of boundary conditions and mantle viscosities will be found that will predict plume motions for Hawaii and Louisville that satisfy both distance and paleolatitude constraints; (b) perhaps plume drift only accounts for a part (e.g., 5°) of the observed paleolatitudes and the remainder should be attributed to





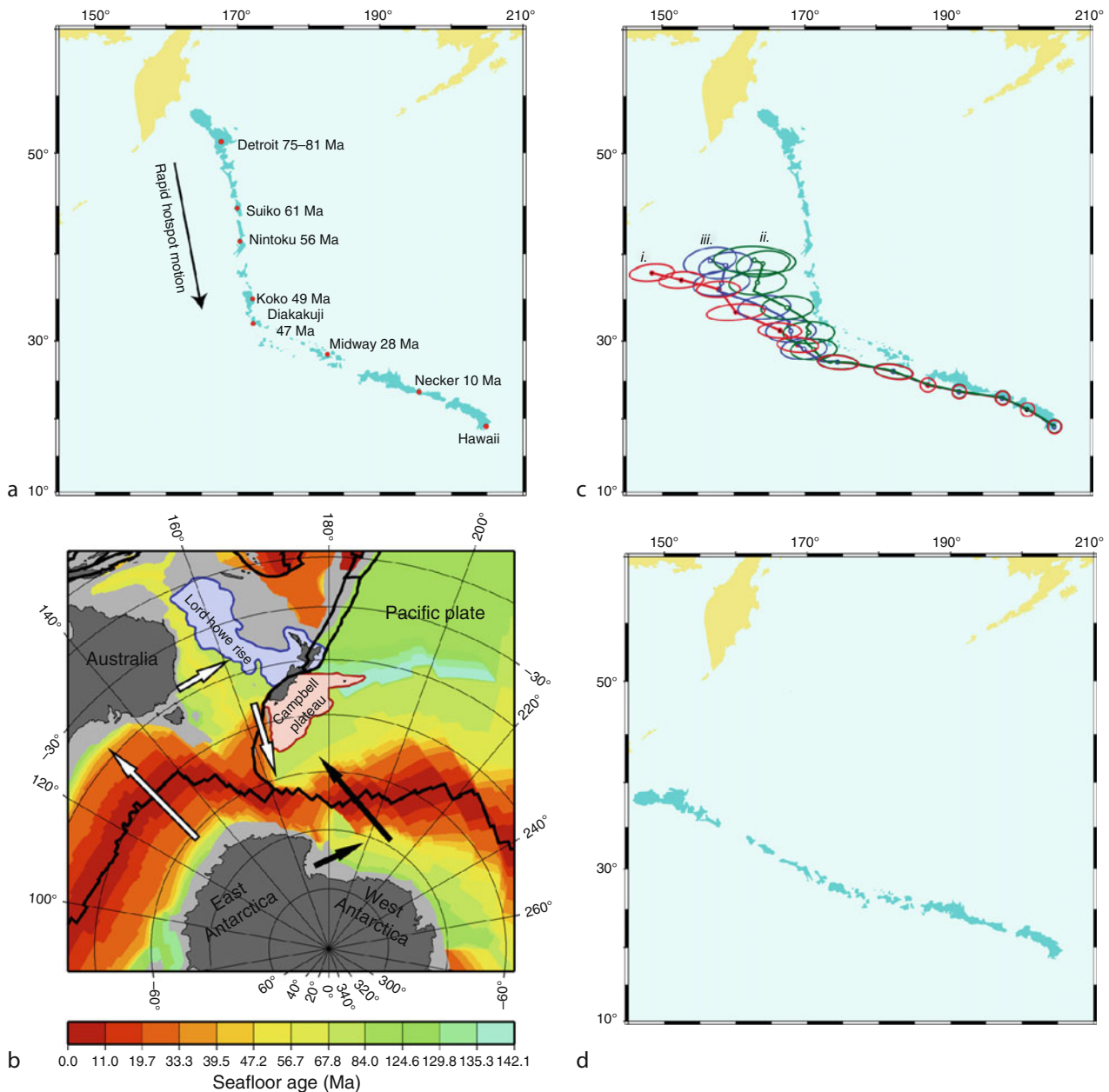
**Plate Tectonics, Figure 5** Examination of distance deviations,  $\Delta(t)$ : the distance between coeval points on different chains minus their present (*fixed*) hotspot separation. The *polygons* represent continuous estimates of  $\Delta(t)$  with assigned uncertainties. *Triangles* show  $\Delta(t)$  for locations of dated rock samples and their estimated coeval locations on other chains. *Dashed line* indicates typical prediction of  $\Delta(t)$  for Hawaii and Louisville from mantle dynamic modeling (Steinberger and Gaina, 2007), with *dotted line* the (t) for the model of Koppers et al. (2004). Scatter due to age uncertainties (not analytic errors, but uncertainties associated with the timescale of volcano building) seems contained within a  $\pm 2^\circ$  window (Redrawn from Wessel and Kroenke, 2009).

TPW (e.g., Duncan and Richards, 1991); or finally (c) the interaction between the Hawaii hot spot and the Kula-Pacific ridge may have lead to the entrapment of plume melt by the ridge (Wessel and Kroenke, 2009). This interaction may have forced surface volcanism due to the plume to erupt closer to the ridge axis (instead of vertically above the plume), particularly after the ridge overrode the plume at  $\sim 78$  Ma. The overall effect would be to distort the oldest age-progression data but also result in more northerly paleolatitudes. While option (c) is not new (Sleep, 1996; Small, 1995; Tarduno et al., 2003) and could perhaps account for  $\sim 4^\circ$  of deviations (which is close to the  $\sim 5^\circ$  we observe), it remains a scenario that is difficult to test. Note, however, that if seamounts formed closer to the ridge than the hotspot location would imply, then the observed age progression would at first be slower but then accelerate as seamounts again begin to form vertically above the hot spot; of course, this scenario reflects the observed Emperor age progression (Sharp and Clague, 2006) and sense of paleomagnetic latitude shifts (Tarduno et al., 2003). Option (b) is a compromise model that allows for most of the HEB change to originate from a plate rather than plume motion change, as supported by contemporaneous global tectonic events (Rona and Richardson, 1978; Wessel and Kroenke, 2008). The implied small amount of TPW ( $< 5^\circ$ ) should be permissible given the

present uncertainties in global paleomagnetic reconstructions (Steinberger and Torsvik, 2008) and the physics of TPW (e.g., Tsai and Stevenson, 2007). The latitudinal shift from TPW would combine with the (reduced) plume motion to satisfy observed paleolatitudes. Finally, option (a) explains the HEB by manipulating plume motions only (Tarduno, 2007; Tarduno et al., 2009); it predicts that most of the north-south APM proposed for the Pacific plate is an artifact of misinterpreting plume drift for plate motion (Figure 6). This model has the benefit of being testable, provided reliable paleolatitudes someday will be determined for the oldest Louisville seamounts. Tarduno et al. (2003) notes the lack of coral reefs on drowned Emperor seamounts north of Koko and cites this as support of more northerly latitudes during the late Cretaceous. However, the absence of evidence is not a strong evidence of absence, and it thus remains possible that the paucity in Emperor seamount reefs is instead linked to palaeoceanographic events (e.g., Grigg, 1997).

### Summary

Reefs that form on continental shelves and the flanks of hotspot islands will experience latitudinal, oceanographic, and climatic changes as the tectonic plates they are part of move over the mantle through geologic time.



**Plate Tectonics, Figure 6** Alternative Hawaii-Emperor geometries. (a) Observed track with ages and inferred period of rapid hotspot motion. (b) Different plate circuits are obtained by using Lord Howe Rise (*white arrows*) instead of connecting West and East Antarctica (*solid arrows*). (c) Differences in predictions of the HEB by projecting Africa APM via different global plate circuits. Regardless of the circuit used, the HEB is poorly predicted. (d) Predicted geometry of the Hawaii-Emperor seamount chain if the Hawaiian hot spot had remained stationary (modified with permission from Tarduno et al., 2009).

Traditionally, models for Pacific APM have had a large northward component during the late Cretaceous, resulting in considerable latitudinal changes for reefs originally in the tropics. However, recent paleolatitude studies from the Emperor seamounts suggest that this northward plate motion is an overinterpretation (or possible a misinterpretation) of the data, and that we instead are seeing the effect of a mostly westward-drifting plate

moving relative to a rapidly southward-moving mantle plume during the 80–47 Ma timespan. If this scenario can be verified by additional high-quality paleolatitude observations from other Pacific chains, in particular the Louisville chain in the south, it will force a major reassessment of all APM models and consequently any geologic hypothesis that relies on plate tectonic control on the evolution of coral reefs.

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## Cross-references

[Darwin Point](#)  
[Oceanic Hotspots](#)

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## PLATFORMS (CEMENTED)

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## Synonyms

Benches; Breccia sheets; Conglomerate platforms; Pavements; Promenades; Rampart platforms; Rock ledges

## Definition

Platforms are horizontal or sub-horizontal, planar surfaces of cemented coral rubble, typically 0.5–1 m thick,

overlying reef flats away from the reef front, and often partly covered by island deposits or mobile sediments.

Cemented platforms are common on the exposed windward side of Indo-Pacific reefs that have islands or *motu* (*Atoll Islands (Motu)*). Platforms are often continuous and have a fairly constant height, though there are variations in surface elevation from reef to reef, and some reefs have platforms at more than one level. Many platforms are exposed above the present level of high tide and have a scarped seaward face or a step down to the reef flat. Inspection of both scarps and surfaces reveal that platforms are made up of poorly sorted, skeletal materials such as coralline algae, mollusks and especially clasts of coral rubble, the latter including branching and massive corals of sizes up to several decimeters. Such rubble is consistent with primary or secondary storm deposits, that have been subsequently cemented into coral conglomerate (Montaggioni and Pirazzoli, 1984) or rampart-rock (Scoffin and McLean, 1978). That is, platforms are the lithified equivalents of coral rubble sheets accumulating on reef flats at the present time.

The broad, planar surfaces of cemented platforms, often called promenades or pavements, led some workers to conclude that they owed their flat top to marine erosion, though now the weight of evidence clearly favors a depositional origin. To facilitate lithification such deposits have to be stationary for some time. They also require some fine interstitial sediment to aid in the retention of saturated waters at grain contacts. Examination of samples from platforms on atolls in French Polynesia and the low wooded islands on Australia's Great Barrier Reef, have shown the cementing medium to comprise acicular aragonite, and/or high magnesium calcite and micrite, preferentially distributed throughout an outcrop, and, between platforms at different levels.

Radiometric ages of cemented platforms associated with modern reef tracts in the Indo-Pacific range from the present through 6,000 year BP. There is, however, a clustering of ages between 3,000 and 6,000 year BP for the extensive coral conglomerates in French Polynesia that reach an elevation of more than 1 m above the present mean tide level; for the widespread upper platform on the Great Barrier Reef; and, for the elevated platforms that underlie most islands on Cocos (Keeling) atoll in the eastern Indian Ocean. In all these cases the platforms have been interpreted as indicating a relative sea level higher than present at the time. By contrast, cemented platforms are minor or absent in Western Atlantic reefs because these reefs have only recently caught up with sea level.

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## Cross-references

Antecedent Platforms  
Conglomerates  
Diagenesis  
Shingle Ridges

## POLEWARD EXTENSION OF REEFS

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### Definition

Coral reefs are primarily tropical but extend into mid latitudes. Poleward extension considers the factors that limit reef growth at the latitudinal limit and the potential for further extension into subtropical waters.

### Introduction

Global climate change poses particular challenges for coral reefs with the expectation that reefs will become increasingly degraded as a consequence of bleaching associated with a rise in sea surface temperatures and reduced calcification resulting from ocean acidification (Kleypas et al., 1999). However, a further possible, and perhaps more positive, response to global warming might be a poleward shift of the latitudinal limit to reef growth (Buddemeier et al., 2004; Precht and Aronson, 2004).

### The latitudinal limit to reef growth

The suggestion of poleward extension of reefs as a result of global warming is based on the premise that it is temperature which imposes the limit to the present distribution of reefs, particularly at their latitudinal limit. Reef growth is prolific in warm tropical waters, but reefs become more marginal where sea surface temperature is around 18°C. The distribution of reefs along the coast of Japan shows a strong relationship with temperature, and there is good correlation between species abundance and sea surface temperature (Veron and Minchin, 1992).

The latitudinal limit to reef formation, however, appears to be related to a series of factors, of which temperature is only one. Competition with other organisms is also significant. For example, macroalgae such as the kelp *Ecklonia radiata*, are extensive on reefs on the Abrolhos Islands (29°S) off Western Australia (Johannes et al., 1983), whereas coralline algae replace corals, particularly at depth on the Elizabeth and Middleton reefs (29–30°S) and Lord Howe Island (31°30'S) in the Tasman Sea (Kennedy and Woodroffe, 2004; Woodroffe et al., 2006). High sediment loads and turbidity may limit other high-latitude reefs, such as those on Inhaca Island (32°54'S), southern Mozambique (Perry, 2003). The highest latitude reef appears to be at Iki Island off Japan, where a reef as far north as 33°48'N has been described (slightly further north than reefs around Bermuda which

occur at 32°50'N), that has withstood winter sea surface temperatures as low as 13.3°C (Yamano et al., 2001).

The composition of carbonate sediments changes at the latitudinal limit to coral-reef formation, with the coralline assemblage (dominated by coral and coralline algae) of tropical waters being replaced by a foramol assemblage (foraminifera and molluscs). There are also significant physical differences. Volcanic islands that lie outside reef seas are exposed to marine abrasion and are generally flanked by steep cliffs and broad near-horizontal shelves (Menard, 1986), whereas a protecting reef attenuates wave energy, and the volcanic landscapes that develop behind such a reef are generally characterized by more gentle hill slopes.

The latitudinal limit is considered a sensitive threshold to coral reef establishment and has been called the Darwin Point (Grigg, 1982). On the Hawaiian Islands, where this threshold marks the change from reefs, such as Midway Atoll and French Frigate Shoals, to the Emperor Seamount chain, the effect is accentuated because of the rate at which the plate is migrating and the rate at which islands are subsiding. The latitudinal limit to reef formation can therefore be a function of the interaction of several factors of which temperature is only one aspect.

### Daly and marginal seas

Reginald Daly believed that Quaternary climate and sea-level changes had been accompanied by substantial shifts in this latitudinal limit to coral-reef development. Daly inferred that the level of the sea had changed throughout the Quaternary as a consequence of the expansion and melt of the ice sheets, and he realized that these sea-level fluctuations had particular implications for reefs. He postulated that there must have been *marginal seas* from which reefs had been eradicated during ice ages, with gradual re-establishment during the postglacial (Daly, 1915, 1934). Sea-surface temperature reconstructions at the glacial maximum, undertaken as part of CLIMAP (1976) revised this view, and demonstrated that there had not been such marked shifts in the 18°C isotherm as had been expected. This implied a less significant contraction of the poleward limits to reef development than inferred by Daly.

### Holocene changes in range

Contrary to the gradual expansion that might have been anticipated under the marginal seas hypothesis of Daly, coring and radiometric dating of reefs close to their latitudinal limit has often revealed that these reefs have shown vigorous growth during the postglacial. In the Abrolhos, for example, there is more than 20 m of Holocene reef that appears to have accumulated at average vertical growth rates of 6–7 mm/year, generally keeping pace with postglacial sea-level rise. Reefs were established at sea level around 6,000 years ago when sea level stabilized close to its present level in this part of the world (Eisenhauer et al., 1993; Wyrwoll et al., 2006). Holocene reefs similarly accreted vertically, and the modern reef



rim morphology had also established by the time of sea-level stabilization, on Elizabeth and Middleton Reefs in the Tasman Sea (Woodroffe et al., 2004). The Holocene history of reef growth on Lord Howe Island implies that a reef structure was in place at least by 5,000 years ago and rapid lagoonal sediment infill was occurring in its lee (Kennedy, 1999; Kennedy and Woodroffe, 2000).

There is also evidence that reefs have been more prolific at the latitudinal limit during mid Holocene than at present. Veron recorded a reef at Tateyama, near Tokyo in Japan, that is now fossil but which contained 72 species 6,000–5,000 years ago, about twice the present diversity of nearby reefs, on the basis of which temperature appears to have been 1.2–1.7°C warmer than present (Veron, 1992, 1995). An early Holocene reef also flourished along 85 km of the southeastern Florida coast, 9,000–7,000 years ago (Toscano and Macintyre, 2003). Coral is presently found in luxuriant communities at several places in the lagoon on Lord Howe Island (Harriott and Banks, 2002); coring and dating of lagoonal sediments, however, implies a phase of more prolific coral growth in mid Holocene (Woodroffe et al., 2005).

### Pleistocene reefs beyond the present latitudinal limit

There is some evidence to suggest that reefs have flourished further poleward at times in the past; for example, limestones of last interglacial age are prominent in Florida. By contrast with the Holocene, greater poleward extent has been interpreted for reefs during the last interglacial from several sites. In Australia, the well-developed reef at Fairbridge Bluff on Rottne Island (Szabo, 1979) suggests more prolific coral than occurs there at present, and that a reef formed, where today only scattered coral communities are found. Greenstein and Pandolfi (2008) indicate that the coral biodiversity of reefs of the Last interglacial age along the coast of southern Western Australia, particularly at the Abrolhos Islands and Rottne Island was considerably greater, with a more tropical assemblage of taxa than that presently found along this coast. They imply that these species might migrate south under future warmer conditions.

Corals occur in last interglacial deposits at Evans Head, on the coast of New South Wales, further south than they presently reach on this coast (Marshall and Thom, 1976). At Lord Howe Island there is some evidence of former Pleistocene reefs revealed by shallow coring in the lagoon (Kennedy et al., 2007), but there is also an extensive fossil reef system in water depths of around 30 m on the shelf around the island (Woodroffe et al., 2006). These provide evidence of conditions warmer than present during the last interglacial in that they reached further south than in the late Holocene.

### Future global warming and the limit to coral growth

Concern about future climate change has reinvigorated concern about the limits to reef growth (Guinotte et al., 2003;

Buddemeier et al., 2004). Discovery in 1998 of the recent establishment of the branching coral *Acropora cervicornis* off the coast of Fort Lauderdale in Florida (Vargas-Angel et al., 2003), contrary to an almost Caribbean-wide trend of coral deterioration, provides one of the first indications that global warming may result in extension of coral range (Precht and Aronson, 2004).

However, it seems that warming may only result in a small increase in potential reef habitat. It is also necessary to take other factors, such as genotypic diversity and gene flow into account, as these can be significant constraints at the latitudinal limits to reef growth (Ayre and Hughes, 2004).

### Summary

In the face of concern about the impact of global warming, particularly in relation to coral bleaching and the threat of thermal stress on tropical reefs, there has been reawakening of interest in marginal reefs. However, it is doubtful if there is much scope for extension of reefs further poleward. Many mid-ocean settings at which reefs are presently marginal represent the limit of land that would be suitable; for example, there are no islands further north of Bermuda or south of Lord Howe Island to which corals could extend. Similarly there is an absence of suitable habitat on many of the mainland coasts beyond the present limit. Where corals are able to colonize, they will be subject to a plethora of other stresses, pollution, sedimentation, and the effects of ocean acidification which are likely to be felt first in these higher latitude settings.

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## Cross-references

[Climate Change and Coral Reefs](#)  
[Daly, Reginald Aldworth \(1871–1957\)](#)  
[Darwin Point](#)  
[Last Glacial Lowstand and Shelf Exposure](#)

## PORITES

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## Synonyms

*Cosmoporites* Duchassaing & Michelotti, 1860;  
*Neoporites* Duchassaing & Michelotti, 1860

## Definition

*Porites* (Phylum Coelenterata, Class Anthozoa, Order Scleractinia) is a genus of colonial, zooxanthellate scleractinian coral.

## Introduction

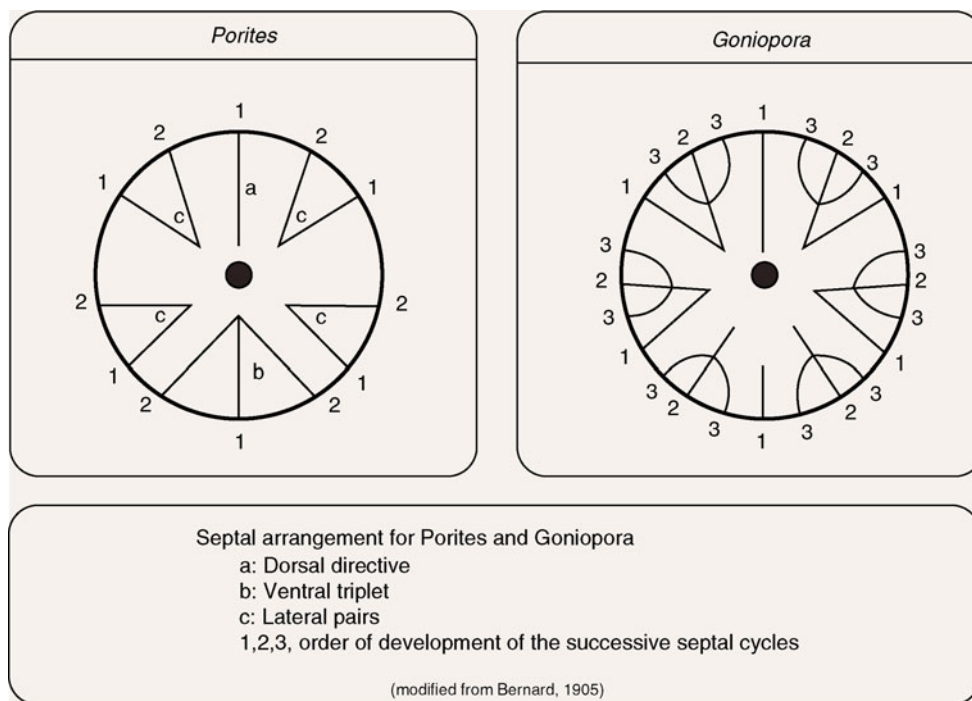
*Porites* are major coral components of reefs, both in the fossil record and in living reefs, in which they can be the most important framework builder. *Porites* can be found in almost all reef habitats. The genus includes large massive species (Figure 1), which are often a dominant component of back reef coral fauna, but also commonly found on the seaward slope and reef flat. Smaller massive specimens also occur in a wide range of reef environments. The genus also includes encrusting and branching species, the latter of which are more common in protected environments, often forming large monospecific stands on the back reef slope and other lagoonal areas. Skeletal banding and isotopic composition of massive *Porites* skeletons provide invaluable records of colony growth rates and past environmental conditions.

## Colony formation and skeletal detail

*Porites* colonies of all shapes are formed by extratentacular budding. Corallites are small (up to 2 mm diameter) with synapticulothecal walls. Corallite septa are arranged in two cycles (Figure 2). They are perforated, being formed by three to four vertical trabeculae loosely connected by horizontal rods. In some septa, the



**Porites, Figure 1** A large massive colony of *Porites lobata* as commonly found in back reef areas. The branching staghorn coral in the foreground is *Acropora nobilis* (Photo: Terry Done).



**Porites, Figure 2** Comparison of the septal plan of *Porites* and the closely related genus *Goniopora*. It is suggested that *Porites* is a derivative of *Goniopora* by reduction and disappearance of the third septal cycle.

innermost trabeculae may develop as pali. Lateral sides of septa are connected by synapticular rings, and there is a columella comprising a single trabecula.

### Palaeontological and taxonomic history

The genus *Porites* was established by Link in 1807, with the Atlantic species *Porites porites* (Pallas, 1766) as type species. Later, Gray (1842) established the family

Poritidae, notwithstanding the fact that the genus *Goniopora*, created by De Blainville in 1830, which includes species dating back from the middle cretaceous, has a longer palaeontological history. The family is a mid-cretaceous derivative of the Actinacididae that, together with the closely related family Microsolenidae, can be traced back in the fossil record to the Triassic-Jurassic boundary. The genus *Porites* is probably derived



from *Goniopora* during the Eocene by a reduction in the number of septa, from 24 (3 cycles) to 12 (2 cycles), and by a decrease in the average number of septal trabeculae, from 4–8 (*Goniopora*) to 3–4 (*Porites*). The one exception to the dodecameral septal arrangement in the genus *Porites* is *Porites decasepta* described by Claereboudt (2006) from the Gulf of Oman.

A closely related monospecific genus, *Stylaraea* Milne Edwards & Haime, 1851 has been considered in the past by some as a junior synonym of *Porites*, but it is now widely accepted that *Stylaraea* is a genus in its own right. The taxonomic position of *Synaraea* Verrill, 1864 and *Napopora* Quelch, 1886 is less clear. The latter, considered as a synonym of *Synaraea* by Wells (1956) itself treated as a subgenus of *Porites* by the same author, is considered as a subgenus of *Porites*, but distinct from *Synaraea* by Veron and Pichon (1982). There could be a case, on the basis of micro-structural considerations, to re-establish *Synaraea* as a genus in its own right. The relationships of two recently described monospecific poritid genera, *Poritipora* Veron, 2002 and *Machadoporites* Nemésio, 2005 (the latter originally named *Calithiscus* by Claereboudt and Al-Amri [2004]), remain uncertain and will require morphometric and molecular genetic analyses to be clarified.

### Geographic distribution

The genus *Porites* is found in both the Atlantic Ocean and the Indo-Pacific Ocean, but there are no species in common between the two areas. There are only four species in the Atlantic Ocean: *P. porites*, which can reach up to 1.2 m maximum colony size, *P. astreoides*, *P. branneri*, and *P. colonensis*, the latter sometimes regarded as a junior synonym of *P. astreoides*. In the Pacific Ocean, more than 140 nominal species have been described, but the number of valid species is unquestionably much lower. A number of species including some with very large, massive colonies that play a major role in the construction of the reef framework are of particular interest due to their large distribution range. They occur from the northern Red Sea south to Madagascar and Mozambique, and in the Pacific Ocean, east to French Polynesia. Many species, however, have a more restricted geographic regional or local distribution (e.g., *P. compressa* restricted to the reefs of the Hawaiian Islands) even though they may be a major and even dominant component of the coral communities within their area of distribution (e.g., *P. harrisoni* in the Arabo-Persian Gulf and *Napopora irregularis* in Polynesia).

### Colony shape and size

*Porites* has attracted the attention of reef biologists by the fact that, for a handful of Indo-Pacific species, individual colonies are massive, and can reach enormous sizes, several meters across and several meters high, up to nearly 10 m (indeterminate growth). These species include *P. lutea*, *P. lobata*, *P. australiensis* and *P. solida*

in particular, and their importance stems from the fact that both in the fossil record and in living reefs (e.g., Done and Potts, 1992), they are often the principal reef framework builders. A larger number of species, however, have generally a much smaller average colony size, sometimes no more than a few centimeters across. Besides the typically massive and often large sized colonies, a variety of colony growth form occurs, including encrusting, lamellar (*P. lichen*), branching (*P. porites*, *P. branneri* in the Atlantic Ocean, *P. cylindrica* and *P. nigrescens* in the Indo-Pacific Ocean). Some species have columnar, nodulose or even more irregular, and at times somewhat ill-defined, growth forms.

### Ecological requirements

#### Temperature

A number of *Porites* species are very tolerant to extremes of seawater temperatures, and hence have a very large geographic distribution. This is the case in particular for the large massive species such as *P. lobata* and *P. lutea*. The latter especially is to be found in seasonally very warm (>32°C), but also very cold (15°C) waters such as in the northern Arabo-Persian Gulf. It also tolerates permanently high (e.g., Gulf of Tomini, Sulawesi, ca. 30°C) or cool waters, down to 21–22°C sea surface temperature (SST) mean annual SST (e.g., Rapa, Austral Islands). In many high latitude reefs, however, the genus is either absent (Kermadec Islands, 29°12' S, mean annual SST 21°C) or represented by only one species: *P. lichen* at Lord Howe Island (31°30' S, mean annual SST 21°C) or *P. lobata* at Easter Island (27°07' S, mean annual SST 22°C). It is to be noted that both high and low extremes of seawater temperatures can trigger a bleaching event (discoloration of the living tissues due to a breakdown of the symbiotic association), which in many instances is followed by a recovery of the colonies affected. Severe bleaching associated with significant SST anomalies, however, may lead to partial or even total mortality of the colonies concerned.

#### Salinity

Like many other coral genera, *Porites* species better tolerate high salinity than low salinity, which limits coral development in the vicinity of estuaries and river mouths. Occasional or accidental decrease in salinity associated with freshwater plumes of flooding coastal streams or rivers may cause partial or total bleaching of *Porites*, which may lead to partial or total mortality of the colonies. A number of species can thrive in areas where salinity is permanently and significantly higher than normal, and up to at least to 42‰, such as the Red Sea and the Arabo-Persian Gulf. Many large massive or columnar species are common throughout the Red Sea (where they were frequently used as building material) and colonies of *P. lutea* and *P. harrisoni* up to several meters across are very common in the coral reefs of Kuwait. The combined effect of temperature and salinity has a synergistic effect on the level of stress and survival of corals, and

*Porites* tolerance to extremes for both factors makes the genus a dominant feature in coral reefs developed in harsh environments.

### Light

In the natural environment, light intensity and quality is associated with other environmental factors such as depth, water transparency, and emersion. Light requirements are, to a large extent, species-specific, but various species of *Porites* can be found at both ends of the light intensity range. Species such as *P. murrayensis*, *P. stephensoni*, *P. lutea*, *P. lobata*, or *P. somaliensis* tolerate exposure to full sunlight at low tide on the reef flats for several hours. Conversely, several large massive species including, *inter alia*, *P. lutea* and *P. lobata* can occur on the deep fore reef slope.

### Sedimentation

In addition to the various mechanisms that have been developed by scleractinian corals to eliminate fine particles which deposit on the colony surface (ciliary currents, tentacular movements), several species in the genus *Porites* produce abundant sheets of mucus, which covers and protects the living tissue, and on which the fine sediment particles get trapped. After some time, generally up to a few weeks, the sheet of mucus is eliminated, thus removing the sedimented particles, and the process may start again. Overall, *Porites* species cope well – within limits – with significant levels of fine particle sedimentation, hence their dominance in areas such as back reef slopes, fringing reefs, or deep embayments.

### Water motion

Despite the fact that many of the species build very large massive colonies, which seemingly would resist strong currents or pounding by breaking swell and waves, large specimens of massive *Porites* are rarely found in areas of very high hydrodynamic energy such as the shallow reef front. This situation may be due to a combination of factors: on the one hand, the area of attachment of massive species on the substratum is much smaller than the large size of the colonies would suggest, and further the colony is often not very firmly adherent to the reef; on the other hand, in such environments, *Porites* is out competed by other (r-strategist) genera such as *Acropora* and *Pocillopora*, or even by crustose coralline algae. As a result, large *Porites* specimens are more commonly found in more protected reef zones such as the reef flat and the reef slopes. Local and regional variability in the abundance and size frequency distributions of massive *Porites* colonies also reflects variability in both the prevailing wave climate and the return period between cyclonic waves strong enough to dislodge corals of different sizes at different depths (Massel and Done, 1993).

### Emersion

A number of *Porites* species found of the reef flat may be fully emerged during low spring tides and exposed to full

sun during daytime, for up to several hours. They include species restricted to that type of environment (*P. murrayensis*, *P. stephensoni*) but also species with a larger cross-reef distribution such as *P. lutea*, *P. lobata*, and *P. australiensis*. The ability of such species to withstand exposure to air, and in particular desiccation, stems from the fact that the three-dimensional structure of the skeleton acts as a wick, pumping water from residual pools of seawater or from water-logged sediment and bringing it to the soft tissue which are as a result kept sufficiently moist. Thus, *Porites* species are often, in terms of vertical distribution, some of the highest corals to be found on the top of the reef buildup.

## Population biology

### Reproduction

The majority of the Indo-Pacific species of *Porites* are gonochoric (separate sexes), spawning gametes, although occasionally a few hermaphroditic polyps or colonies are found, and they reproduce only once a year (Harrison and Wallace, 1990). In contrast, the Atlantic representatives of the genus are hermaphroditic and up to nine reproductive cycles have been recorded for *P. astreoides* (Szmant, 1986). This situation can be explained by the fact that the faunas of the two regions have been separated for more than 10 million years, hence there has been evolutionary divergence resulting in contrasting sexual patterns. Little is known of size/age at first reproduction. Harriott (1983) gives a colony diameter of less than 8 cm for gravid *P. australiensis* and *P. lutea* (which have massive growth forms) For the branching *P. astreoides* in Panama, first reproduction occurs when the average branch length reaches 8.4 cm, the smallest reproductive colony having a dimension of 3 × 2 cm (Soong and Lang, 1992). However, polyp fecundity in female colonies is correlated with branch thickness but not with age (Chornesky and Peters, 1987). For branching species in general, the tips of the branches are infertile (juvenile polyps) as are polyps at the base of the colonies. There are no data specifically for *Porites* species on the duration of the planktonic larval stage and larval dispersal. With respect to larval settlement, laboratory experiments have shown that for *P. porites*, larval settlement is patchy as a result of aggregated settlement behavior (Goreau et al., 1981). Like many other corals, growth rates in the first year after settlement are low and mortality very high. Quantitative data are scarce: Vaughan (1912) gives a figure of 4 × 3 mm after a year for the slowest growing *Porites* spat, with up to 14 × 23 mm for an agglomeration of six planulae.

Among the various modes of asexual reproduction, breakage, survival, and subsequent regrowth of coral fragments are common occurrences for scleractinian corals (Highsmith, 1982). This reproduction strategy occurs in large, massive, *Porites* species (Done and Potts, 1992) but it is probably more frequent in columnar species and branching species such as *P. cylindrica* and *P. nigrescens* on the Great Barrier Reef (Resing and Ayre, 1985) and

*P. compressa* in Hawaii (Hunter and Kehoe, 1986). At population level, Hunter (1985) presented evidence of predominantly clonal populations for *P. compressa* in Hawaii, but at a broader geographic scale the relative importance of asexual reproduction has not been fully assessed for most of the dominant, reef-building species.

### Growth and growth rates

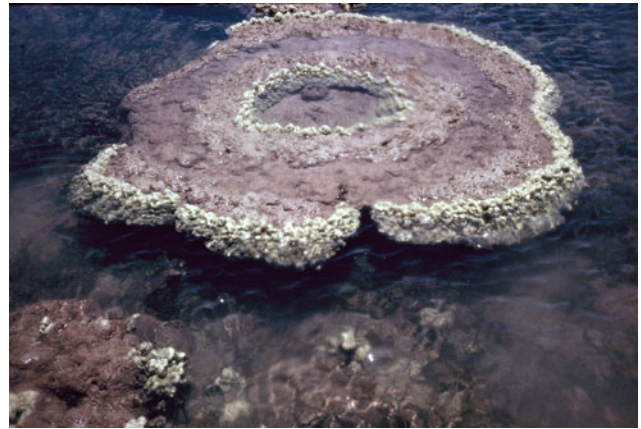
Growth in the genus *Porites*, in particular retrospective growth in massive species, has been the subject of particular attention. This attention reflects their paramount importance as primary reef builders, and hence their role in coral reef development and maintenance. Growth in massive *Porites* is particularly amenable to a study by radiographic techniques (“density banding”), which rely on the seasonality in the density of calcium carbonate deposition. In most cases, yearly skeletal accretion includes a dark band (period of intense  $\text{CaCO}_3$  deposition) and a lighter band (period of lower  $\text{CaCO}_3$  deposition). For a general review of coral growth, refer to Buddemeier and Kinzie (1976). Radiographic analyses of density banding in cores obtained from large massive *Porites* show that:

- Many large colonies are more than 100 years old, and some even reach an age of 700 years or more.
- Average growth rates (radial increment) vary between 8 and 18  $\text{mm year}^{-1}$  for unstressed corals, with extremes of ca. 3  $\text{mm year}^{-1}$  for *P. lutea* at Enewetak (Highsmith, 1979) and 22.7  $\text{mm year}^{-1}$  for *Porites* sp. on the Great Barrier Reef (Lough and Barnes, 2000).

For massive *Porites* with a 0.2–0.5 m colony height range, growth rates along the vertical axis ( $13.0 \pm 3.4 \text{ mm year}^{-1}$ ) are significantly higher than along the horizontal axis ( $10.9 \pm 3.2 \text{ mm year}^{-1}$ ) (Lough and Barnes, 2000). In the particular case of colonies living on the reef flat, and especially in areas of significant tide range, however, the situation may be reversed. After some time, the vertical growth of the massive and often hemispherical colony becomes limited by the emersion of the top of the colony at low tide, while it continues to grow horizontally, taking an irregular disc shape. The upper surface dies and sometimes becomes the settlement site of other corals, or may be the subject of intense bioerosion, leading to an excavation in the central (older) part of the colony. Given suitable hydrodynamic conditions, the living tissue can grow again on the sides of the excavation. Because of its gross morphological similarity with that of an atoll (at a much smaller scale), such formations have been named “micro-atolls” (Figure 3).

Environmental factors other than emersion that control the growth rates of *Porites* include light, temperature, turbidity, and depth (which itself integrates the action of light, water motion, rates of sedimentation – see “Corals: Environmental Controls on Growth”).

In broad terms light enhances calcification, and its variations with season and depth account for some of the variability recorded in growth rates. The physiological



**Porites, Figure 3** A micro-atoll of *Porites lutea*, emerged during a low spring tide on a reef flat. Such micro-atolls can have a diameter of several meters.

and biochemical processes involved in calcification are not yet fully understood and may include a decoupling of calcification from photosynthesis and possibly an intrinsic rhythm of calcification.

Growth rates of *Porites* are significantly related to average sea surface temperature, which is one of the most important factors controlling growth rates. Lough and Barnes (2000) report that in the Indo-Pacific region, including the Hawaiian Archipelago, annual extension rates increase by 3.1  $\text{mm year}^{-1}$  for each  $1^\circ\text{C}$  increase in average annual SST, within the range  $23\text{--}29^\circ\text{C}$ . They further surmise that on the Great Barrier Reef, sensitivity of calcification rates to SST suggests that growth rates of *Porites* will – at least initially – increase as a result of global warming. There is some evidence that calcification rates did increase for much of the twentieth century, but recent findings suggest that the trend has been dampened post-1985, possibly due to a decrease in aragonite saturation levels linked to ocean acidification (De'ath et al., 2009).

As mentioned above, other factors such as depth, water motion, fine particle sedimentation, and pollutants play a role in combination in controlling growth rates of *Porites*. However, no clear picture emerges when considering, for instance, inshore–offshore gradients. Extension rates decrease with distance from shore on the Great Barrier Reef and in Thailand, but increase with distance from shore in Jakarta Bay and in Mayotte. In the latter case, however, Priess et al. (1995) also indicate a decrease in growth rates with depth on the outer slope of the barrier reef.

Through the process of calcification, corals incorporate a number of trace elements (various stable isotopes, particularly of oxygen and carbon, fulvic acids, etc.) in their skeleton throughout their lives. Their time of incorporation can be precisely determined, providing a means to characterize the environment at that time. Long-lived species such as massive *Porites*, in particular, therefore constitute an archive of past climatic and environmental



conditions that can span several centuries and are a precious tool for paleoclimatic reconstructions (e.g., McGregor and Gagan, 2003).

## Mortality

Little is known on the natural mortality of the various species of *Porites*. While some massive species can live for several centuries, the situation is very different for many other massive species that never reach large sizes, and for branching species.

Mortality can be the result of catastrophic events such as tropical storms or cyclones (see “*Tropical Cyclone/Hurricane*”). These events can bury some colonies under thick layers of sediment and dislodge others, sometimes throwing them onto the reef top or rolling them into unviable depths down the reef slope (Massel and Done, 1993). Large *Porites* colonies, if overtopped in well-illuminated habitats, rarely die completely. Partial mortality may be observed on the parts of the colonies that come into contact with the substratum, but the rest of the colony may continue to live and grow normally, even colonizing the dead part of the former under surface. Tropical storms and cyclones may be associated with freshwater runoff from flooding coastal rivers. Decrease in salinity, particularly if maintained over significant periods of time, is likely to induce a bleaching of the colonies (i.e., a breakdown of the symbiotic association), which may lead to partial or total mortality (Brown, 1997).

Extreme temperatures, particularly high SSTs at the end of the warm season are a frequent cause of coral bleaching. In general, *Porites*, particularly the large-sized species, are more resistant to extremes of temperatures than many other coral genera, e.g., *Acropora*, *Pocillopora*, *Galaxea*, or *Pavona* (Marshall and Baird, 2000). However, bleaching resulting from a temperature stress and leading to partial or total mortality has been recorded for a number of *Porites* species. There are also a number of other causes of bleaching which may affect *Porites*, in particular heavy sedimentation (or re-suspension) of fine particles, a situation commonly found in inshore reefs (see *Turbid-Zone and Terrigenous Sediment-Influenced Reefs*), and reefs affected by anthropogenic disturbances near the shore line (dredging, excavating, in-filling).

Like many other coral genera, *Porites* can be affected by natural enemies which impair the integrity of the colonies to various degrees. Infestations of boring mollusks (*Lithophaga*), sponges (*Cliona*, *Microciona*), polychaetes (*Spirobranchus*), sipunculid worms, and several species of cirripeds are known to disturb natural growth and at times modify the shape of the colonies. In many instances, however, such infestations do not lead to partial or total mortality of the colonies infested but may result (particularly in the case of cirriped infestation) in the development of a pink blotch syndrome. One specialized coral predator, the crown of thorns starfish *Acanthaster planci*, when present in large numbers, may cause up to 90% hard coral mortality in an area. *Porites*, however, generally becomes

the prey of *Acanthaster* only after most other hard coral species have been consumed. It is possible that the massive growth form with a comparatively smooth surface of *Porites* makes it less easy to be climbed on by *Acanthaster*, and the possibility of chemical defense has also been suggested (Barnes et al., 1970). Nevertheless, recurrent *A. planci* outbreaks can cause major depletions of reef-wide *Porites* populations that cannot necessarily be fully restored between outbreaks, with the potential to cause a rapid run-down of their abundances and size-structure (Done, 1988). Black band disease, due to an infection by the cyanophyte *Phormidium corallyticum*, has been reported on *Porites* spp. on the Great Barrier Reef, but its incidence remains very low, compared to that on other coral genera, most notably *Acropora*.

## Summary

The importance of the genus *Porites* on coral reefs reflects to a large extent the survivability of a handful of very environmentally tolerant species. The genus occurs in both the Atlantic and Indo-Pacific, and it is in the latter where it produces – by scleractinian coral standards – among the largest and most long-lived coral colonies. *Porites* is a predominant reef frame builder, and an excellent archive of recent past environmental conditions and climate. Longevity, resulting from its capacity to withstand natural and anthropogenic stress and impacts better than most other genera, has also brought the genus to its position of dominance. Massive colonies of *Porites* are a good example of a “long-lived species that structures coral reef systems” (Cameron and Endean, 1985).

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## Cross-references

[Acanthaster Planci](#)  
[Ecomorphology](#)  
[Forereef/Reef Front](#)  
[Geomorphic Zonation](#)  
[Lagoons](#)  
[Microatoll](#)  
[Reef Flats](#)  
[Sclerochronology](#)  
[Temperature Change: Bleaching](#)  
[Tropical Cyclone/Hurricane](#)

## POROSITY VARIABILITY IN LIMESTONE SEQUENCES

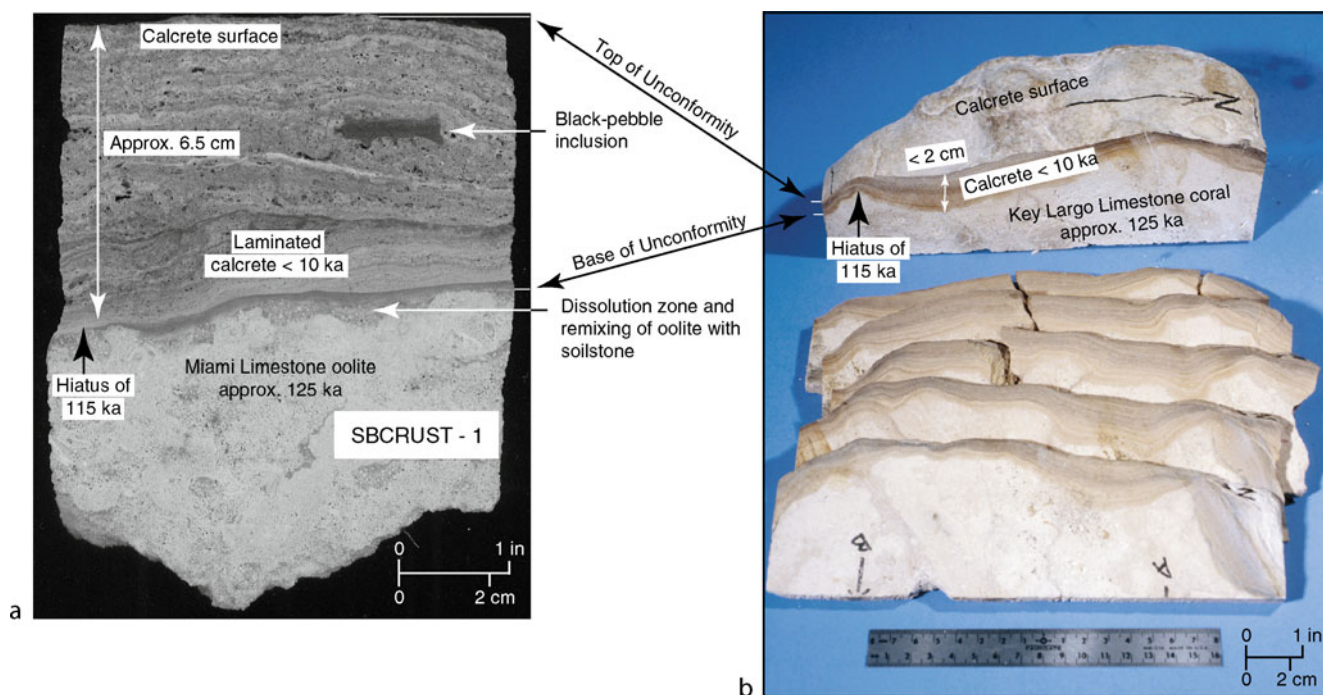
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## Synonyms

Aquifer system; Aquifer vs. aquiclude vs. aquifuge (confining bed); Fenestrate vs. non-fenestrate (non-perforate); Hydrostratigraphic unit; Karst in Florida Boulder Zone; Large voids in fossil coral reef; Porosity affects permeability (fluid flow); Small grain-supported interstitial space in rock or soil

## Definition

Porosity is the state of being porous, as measured by the percentage of bulk volume of a rock or soil that is occupied by space, whether isolated or connected. In hydrocarbon-bearing limestone settings, subsurface porous strata containing the oil or gas usually underlie non-porous caprock through which hydrocarbons cannot pass. In karst-limestone settings, subsurface freshwater aquifers beneath caprock can become contaminated by saltwater intrusion during periods of drought. Islands of the Florida Keys consist of two types of emergent 125-ka limestone, a highly porous fossil coral reef with



**Porosity Variability In Limestone Sequences, Figure 1** (a) Core slab from the Saddlebunch Keys (lower Florida Keys) shows thick calcrete unconformity on top of Miami Limestone oolite. (b) Cut rock sample from the Key Largo Waterway on Key Largo (upper Florida Keys) shows the same calcrete unconformity as it developed on top of Key Largo Limestone coral reef (reprinted from Lidz et al., 2007, with permission). This figure (a and b) is also cited in the Definition and figure caption for the entry entitled, Calcrete/Caliche. See Figure 2a in entry entitled, Florida Keys, for locations of the Saddlebunch Keys and the Key Largo Waterway.

large voids and a less porous oolite with small grains and interstices. Both limestones are capped by impervious laminated Holocene calcrete whose dimensions differ greatly (Figure 1a and b). Porosity variability in the limestones is thought to be the cause. The less permeable oolite retained rainfall moisture longer, allowing longer periods of calcrete buildup. Reddish and brownish layers in both illustrated calcrete samples represent periods of influx of non-carbonate minerals on African dust. The hiatus or gap in these rock records represents an interval of >115 kyr during which no marine or terrestrial deposition is recorded.

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### Cross-references

[Airborne Dust Impacts](#)  
[Calcrete/Caliche](#)  
[Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity](#)  
[Density and Porosity: Influence on Reef Accretion Rates](#)

[Emerged Reefs](#)  
[Florida Keys](#)  
[Oil and Gas Reservoirs and Coral Reefs](#)  
[Ooids](#)  
[Reef Drilling](#)

## POSTGLACIAL TRANSGRESSION

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### Synonyms

(Last) Deglacial sea-level rise; Post glacial sea-level rise

### Definition

The post-glacial transgression is the rise in sea level from –120/130 m to present position in the period 19–6/5 kyears, and caused by global glacial melting.

### Reef growth mode, tectonic and reconstruction of sea-level variations

The corals are reliable markers of sea level (see entry [Sea-level Indicators](#)) and several curves of the deglacial



sea level were proposed using their dating (see entry *Uranium Series Dating*). The reconstruction of these curves must take into account several parameters including the reef-growth patterns and the tectonic parameters (rate of vertical motions).

The mode of reef growth must be examined with accuracy because the organisms respond differentially to more or less rapid sea-level rise (see entries *Corals: Environmental Controls on Growth* and *Sea Level Change and Its Effect on Reef Growth*). Moreover, the corals can have a broad living bathymetric range. Three growth mode strategies were defined by Neumann and Macintyre (1985) and Davies and Montaggioni (1985): (1) the “keep-up” growth mode strategy characterizes the reefs able to maintain pace with sea-level rise, composed of relatively shallow-water and high-wave energy organisms; (2) the “catch-up” growth mode strategy characterizes the reefs, which were not initially able to keep pace with sea-level rise, but caught up as or after stabilizations of the sea level. The communities are made of relatively deeper, less wave-resistant and less light-intensity organisms, progressively replaced upwards by relatively shallow-water and high-wave energy resistant organisms; (3) the “give-up” mode strategy, the organisms are not able to compensate the sea-level rise and gradually drowned.

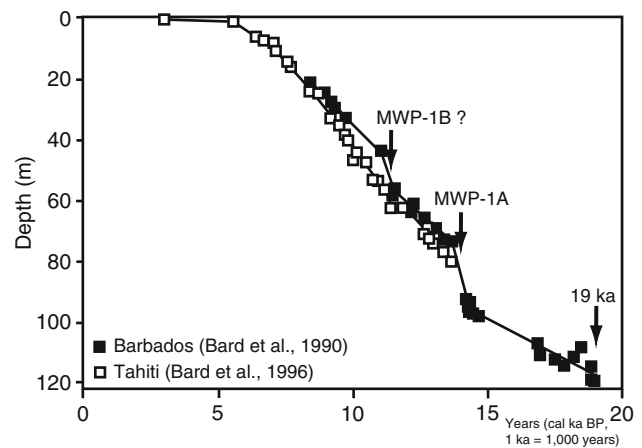
The corrections due to the tectonic parameters must also be taken into account. The uplift rate in the island arc sites and the subsidence in the intra-plate sites or in the continental margins, must be used to correct the sea-level curves. Moreover, the correction due to the loading of the ocean floor by the meltwater (hydro-isostatic effects) should also be taken into account (see Lambeck et al., 2002).

### The sea-level curves from the last deglacial rise

Corals can be used to reconstruct entirely or partly the deglacial sea-level rise curves. Several areas were investigated in the uplifted sites (island arcs) from Barbados (from 22.1 to 7.4 ka, 1 ka = 1,000 years (Fairbanks, 1989; Bard et al., 1990; Peltier and Fairbanks, 2006) and Papua New Guinea (Cutler et al., 2003 and from 13.1 to 8.3 ka, see Edwards et al., 1993) and in the subsiding site of Tahiti in French Polynesia (from 13.8 to 2.8 ka, Bard et al., 1996, 2010, Figure 1). Additional data are available in South-West Pacific in Vanuatu (from 22.6 to 6.6 ka, Cabioch et al., 2003) and in North-West Pacific in the Ryukyus (Sasaki et al., 2006). In the first curve using coral dating presented by Fairbanks (1989), two episodes of Meltwater Pulses (MWP) were identified, the MWP 1A at around 14 ka and the MWP 1B at 11.3 ka. Although these events will be presented in the entry “*Meltwater Pulses*”, a short description is also given below.

### Episodes of rapid sea-level rise

During the last deglacial sea-level rise, several episodes of rapid rise occur. The existence, the timing, the magnitude, and the cause of some of these sharp rises are however still



**Postglacial Transgression, Figure 1** Sea level curves deduced from the coral dating in Barbados and Tahiti (Modified after Bard et al., 1996).

debated. Three episodes have been proposed: the 19 ka event, the MWP 1A, and the MWP 1B. Some of these episodes were attributed to episodes of Meltwater Pulses (MWP, see Chapter *Meltwater Pulses*), but the source needs to be clearly identified. According to some authors, an additional event should also be considered at around 7.5 ka (Blanchon et al., 2002; Yu et al., 2007; Siddall et al., 2010).

### The 19 ka event

The 19 ka event defined in the Bonaparte Gulf (Australia) by Yokoyama et al. (2000), at the end of the Last Glacial Maximum (LGM) is characterized by a rapid sea-level rise of 10–15 m. Clark et al. (2004) confirm the occurrence at 19 ka of a rapid 10-m-sea-level rise deduced from the sediment analyses of the Irish Sea. Drowning of reefs in the Marquesas (Cabioch et al., 2008) at this time adds further support to such an event. The cause of this 19 ka event is attributed by Clark et al. (2004) to the melting of at least one Northern Hemisphere ice sheet but this needs to be constrained by further geochronological data (Clark, 2009).

### The MWP 1A

The second event at 14.5 ka is marked by a rapid sea-level rise of 20 m in less than 500 years. It is reported at various sites but the timing and the source are also still actively debated. Fairbanks (1989) first reported this event in the Barbados, but it is also observed in numerous sites from the Pacific and Atlantic Oceans. In the Sunda shelf, the sea level increased rapidly by 16 m from 14.6 to 14.3 ka. An apparent discrepancy in the timing of the MWP 1A between Barbados (Fairbanks, 1989; Bard et al., 1990; Peltier and Fairbanks, 2006), Papua New Guinea (Cutler et al., 2003), and Bonaparte Sea (Yokoyama et al., 2000) reported in Stanford et al. (2006) is probably due to the fact that the living bathymetric range of dated corals was

not taken into account to correct the sea-level curve (Clark, 2009). The reef growth mode needs always to be considered. Nevertheless, Peltier and Fairbanks (2006) highlight the fit between the record from Barbados and Sunda shelf. The possible sources of the MWP 1A are also highly debated. The ice melting from Northern Hemisphere is probably accompanied by a contribution of the Antarctica (Clark, 2009), although Peltier and Fairbanks (2006) consider that Antarctica is not a significant contributor of the source of the MWP 1A. All these discussions emphasize the need to acquire new data to improve the interpretations and the models.

In addition to the study of living reefs, studies of drowned reefs also sheds light on the MWP-1A event. In Hawaii, the drowning of the 150-m-coral reefs, constrained by its datation from 15.2 to 14.7 ka, is interpreted by Webster et al. (2004) as caused by the rapid sea-level rise of the MWP 1A. Similar observations can be made in the Marquesas archipelago, the drowning of the coral reefs ranging from 110 to 95 m and dated from 16.2 to 14.5 ka (Cabioch et al., 2008) can be also a consequence of the rapid sea-level rise of the MWP 1A. Similar sites of drowned reefs can be observed in various regions but at this day, no dates were performed and we cannot conclude on the causes of the drowning.

### The MW 1B

The MWP 1B was defined in Barbados by Fairbanks (1989). Nevertheless, the existence of such an event is still debated and discussed. Recently, Peltier and Fairbanks (2006) indicated that the source from Antarctica of the MWP 1B is assumed by the model ICE-nG. Although the timing and the magnitude of the MWP 1B cannot be confirmed by the observations of the deglacial sea-level curves from Papua New Guinea (West Pacific) and Tahiti (South Pacific), this event seems to be recognizable in the West Pacific in Vanuatu (Cabioch et al., 2003) and in the Indian Ocean in Mayotte island (Zinke et al., 2003). Although the magnitude of the MWP 1B, if real, seems to be smaller than in the MWP 1A, significant changes can be observed in reef growth patterns in Vanuatu at this period (Cabioch et al., 2003): it appears that around 11.5 ka, relatively shallow-water communities were replaced by relatively deeper organisms, that is, the reef was not able to maintain pace with sea-level rise and the water depth strongly increased over the reef. Similarly, in the Marquesas archipelago, reefs at depths between 80 and 68 m and dated at around 12.4 ka seem to have been drowned (Cabioch et al., 2008). However, the existence of this event is still discussed and debated because most of coral reefs continued to grow during this period as for example in Tahiti (Bard et al., 1996). New uranium-thorium dates were recently obtained on corals from Tahiti providing a new Tahiti sea-level record (Bard et al., 2010). This new record points out no significant change in the sea-level rise during the period attributed to the MW 1B, but a slower rate of sea-level rise during the Younger Dryas (11.6–12.9 ka).

### The 7.5 ka event

In 2002, Blanchon et al. reported the occurrence of a 6-m-rapid jump of the sea level at around 7.5 ka. Such an event at this period is rarely reported (Yu et al., 2007) and needs to be validated but many modern coral reefs settled after this date, especially in the Pacific (Montaggioni, 2005). Additional data must be collected regarding the occurrence of this event.

### Prospects

In 2006, in the framework of the international program IODP (Integrated Ocean Drilling Program), the Tahiti Sea Level Expedition 310 was conducted by G. Camoin, Y. Iryu, and D. McInroy in Tahiti to improve our knowledge on the last deglacial sea-level rise, to analyze the SST changes during this period, and to define the reef development controlled by these two last factors (Camoin et al., 2007). Several cores were collected in 22 sites from three areas. One of the objectives of this expedition was to define the sea-level variations over the period from 20 to 10 ka. At this day, the results are not yet published but the data probably will improve our knowledge on the timing and the sources of the MWP. Another IODP expedition is currently in progress in the Australian Great Barrier Reef (Expedition 325) focused on similar topics, that is, to analyze the pattern of the last deglacial sea-level rise far from the polar sites and to provide data to solve the timing and the magnitude of the brief and rapid increases of sea-level rise (Webster et al., 2009).

### Summary

The postglacial transgression is of broad interest, interacting with the reef growth patterns and the history of the reef development. The last sea-level rise is marked by episodes of rapid increase. Some of them are clearly attributed to melt water pulses but the timing, the magnitude, and the melting source are still debated and discussed. Additional data in sites tectonically stable and far from the polar sites are required to solve these questions. The corals and the coral reefs are reliable contributors and the key to reconstruct with accuracy the last deglacial sea-level curves, the timing and magnitude of the brief and rapid episodes of sea-level rise on condition that the bathymetric range of coral dated can be estimated and the reef growth mode defined.

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## Cross-references

Glacio-Hydro Isostasy  
 Meltwater Pulses  
 Radiocarbon ( $^{14}\text{C}$ ): Dating and Corals  
 Sea Level Change and Its Effect on Reef Growth  
 Sea-level Indicators  
 Submerged Reefs  
 Uranium Series Dating



# Q

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## QUOY, JEAN RENE (1790–1869) AND GAIMARD, JOSEPH PAUL (1796–1858)

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Following the Napoleonic Wars, further scientific investigation of the southern oceans by the competitive powers of England and France resumed, although the French expedition 1800–1804 under Baudin in command of *Le Géographe* and *Naturaliste* was a fiasco marred by scurvy of his crew and conflict with the naturalist François Auguste Péron. Since the British were making important gains in the south Pacific the French renewed their interests and in September 1817 *L' Uranie* under the command of Louis Claude Desaulles de Freycinet sailed from Toulon, carrying aboard surgeon and zoologist Dr. Jean René Constand Quoy and assistant surgeon and zoologist Joseph Paul Gaimard who were to make significant contributions to helping solve the puzzle of atoll and coral reef formation in the otherwise great open spaces of the tropic oceans.

By the early nineteenth century, reef atoll formation was known to have come from small animal polyps, but many other questions, however, remained unanswered. Given the enormous depth of the surrounding waters, unable to be sounded by the technology of the times, how had polyps established themselves in the first place? Upon what foundations had they erected their limestone structures? What was the nature of that “instinct” proposed by Forster by which “the animalcules forming these reefs... shelter their habitation from the impetuosity of the winds?” Most importantly, why were the atolls circular in shape – many being miles in diameter – readily confirmed from the crow’s-nest of the exploring ships?

In that period of extensive reef investigation from 1817 to 1820, chiefly to the Mariana, Hawaiian and Dutch East

Indies island groups, the two zoologists offered an explanation from their findings in 1824 entitled *Mémoire sur l'Accroissement des polypes lithophytes considéré géologiquement* (“Geological aspects of coral formation”). In that joint paper they argued from their extensive examination of reefs in Pacific tropical waters that it would be a mistake to ascribe all atoll formation to polyps alone, growing up from the ocean floor. Rather, they believed that coral reefs are surface features that have as a base the same element, the same minerals which concur to form all the known islands and continents... that [in effect] they build their dwellings on the submarine rocks, enveloping them entirely, or in part, but properly speaking they do not form them. Thus, all these reefs, they concluded, “are, in our opinion, platforms arising from the conformation of the primitive surface.”

Tragically, on the return voyage approaching Patagonia *L' Uranie* was wrecked on an uncharted reef, and although the ship was beached, their supplies and a large part of their natural history specimens were lost as the violent seas rapidly destroyed the foundering vessel. Eventually, however, they were rescued by a passing American vessel which carried them and their scientific specimens to Montevideo from where, when they arrived in France their specimens – mammals, birds, fish and insects – were received by the Academy of Sciences with considerable admiration. What created intense interest were the jars of preserved marine creatures, particularly polyps and invertebrates, and the drawings made by the artists and naturalists of the expedition.

In 1826 Quoy and Gaimard were to sail again on a voyage of exploration to the south Pacific aboard the frigate *L' Astrolabe* under the command of Jules Sébastien César Dumont d'Urville where they were able to continue their observations on coral formations and the taxonomic distinction between those described by Peyssonnel as “supple and pliant” and “stony, hard, inflexible”.

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# R

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## RADIOCARBON ( $^{14}\text{C}$ ): DATING AND CORALS

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### Definition

Radiocarbon or  $^{14}\text{C}$  is the radioactive isotope of carbon. It is the basis for radiocarbon dating and is useful for dating materials that contain carbon back in time to around 50,000 years ago.

### Introduction

There are three *isotopes* of carbon found in nature. They are carbon-12, carbon-13, and carbon-14. Carbon-12 accounts for  $\sim 99.8\%$  of all carbon atoms, carbon-13 accounts for  $\sim 1\%$  of carbon atoms while  $\sim 1$  in every 1 billion carbon atoms is carbon-14. Hereafter, these isotopes will be referred to as  $^{12}\text{C}$ ,  $^{13}\text{C}$ , and  $^{14}\text{C}$ .  $^{14}\text{C}$  is radioactive and has a *half-life* of 5,730 years. The half-life is the time taken for an amount of a radioactive isotope to decay to half its original value. Because this decay is constant it can be used as a “clock” to measure elapsed time assuming the starting amount is known. A unique characteristic of  $^{14}\text{C}$  is that it is constantly formed in the atmosphere (Figure 1).

### Production and decay

$^{14}\text{C}$  atoms are produced in the upper atmosphere where neutrons from cosmic rays knock a proton from nitrogen-14 atoms. These newly formed  $^{14}\text{C}$  atoms rapidly oxidize to form  $^{14}\text{CO}_2$ . They are chemically indistinguishable from  $^{12}\text{CO}_2$  and  $^{13}\text{CO}_2$ . They then join the earth's carbon cycle. Plants incorporate  $^{14}\text{C}$  during photosynthesis and organisms that eat plants take up this  $^{14}\text{C}$ .  $^{14}\text{C}$  gets into the dissolved inorganic carbon pool in the oceans, lakes, and rivers. From there it gets into shell,

corals, and other marine organisms. When a plant or an animal dies, it no longer exchanges  $\text{CO}_2$  with the atmosphere (ceases to take  $^{14}\text{C}$  into its being). This starts the radioactive decay “clock.”  $^{14}\text{C}$  decays by emitting an electron, which converts a neutron to a proton, converting it back to its original  $^{14}\text{N}$  form.

### History of radiocarbon dating

Willard Libby invented radiocarbon dating in the late 1940s. This invention revolutionized science as a means to provide ages to events over the past  $\sim 50,000$  years. Libby was awarded the Nobel Prize for chemistry for this contribution. His first publication showed the comparisons between known age samples and radiocarbon age (Libby et al., 1949; Libby, 1952).

### Measuring $^{14}\text{C}$

To obtain the radiocarbon age of a sample one must determine the proportion of  $^{14}\text{C}$  it contains. Originally, this was done by what is known as “conventional” methods, either proportional gas counters or liquid scintillation counters. The gas counter detects the decaying beta particles from a carbon sample that has been converted to a gas ( $\text{CO}_2$ , methane, and acetylene). A liquid scintillation measurement needs the carbon to be converted into benzene, the instrument then measures the flashes of light (scintillations) as the beta particles interact with a phosphor in the benzene. The main limitation of these techniques is sample size, and hundreds of grams of carbon are needed to count enough decaying beta particles. This is especially true for old samples with low beta activity. In the late 1970s and early 1980s, the dating of small samples became possible using accelerator mass spectrometry (AMS; Muller, 1977; Nelson et al., 1977). This method needs less than 1 mg of carbon and directly measures the abundance of the individual ions of carbon ( $^{14}\text{C}$ ,  $^{12}\text{C}$ , and  $^{13}\text{C}$ ).



To obtain a radiocarbon age the sample activity or the  $^{14}\text{C}/^{12}\text{C}$  ratio must be compared to a standard material of known age. All radiocarbon laboratories either standardize to the US National Bureau of Standards Oxalic Acid I (OX-I), which is derived from Sugar Beets in grown in 1955 or a secondary standard NBS OX-II (grown in 1977) or Australian National University Sucrose (ANU), which is sugar from the 1974 sugar cane growing season in Australia. Both the OX-II and ANU have been extensively cross calibrated to OX-I and can be used to normalize a sample for radiocarbon dating. The absolute radiocarbon standard is 1890 wood, the OX-I standard has an activity of 0.95 of this wood. The definition of year “0,” “modern” or “present” is 1950, there is no real reason for this other than to commemorate the publication of the first radiocarbon dates.

The radiocarbon age is determined by the equation

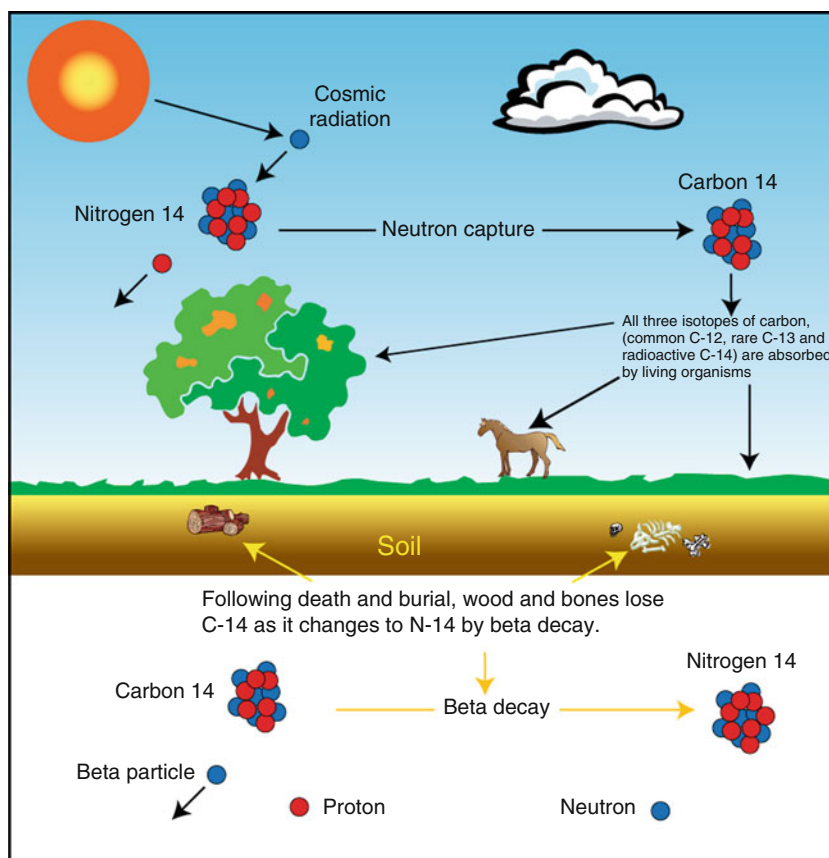
$$t = -8,033 \ln(\text{Asn}/\text{Aon})$$

where  $-8,033$  represents the mean lifetime of  $^{14}\text{C}$  (Stuiver and Polach, 1977), Asn is the activity in counts per minute of the sample, and Aon is the counts per minute of the modern standard. A variant of this equation is also used when

the samples are analyzed by AMS. All radiocarbon ages are normalized to a  $\delta^{13}\text{C}$  of  $-25\text{‰}$  relative to Pee Dee Belemnite (PDB).

### Calibration to time

In the 1950s, it was observed that the radiocarbon time-scale was not perfect. The age of known artefacts from Egypt were too young when measured by radiocarbon dating. A scientist from the Netherlands (Hessel de Vries) tested this by radiocarbon dating tree rings of known ages (de Vries, 1958). He noted some discrepancies indicating that radiocarbon results would need to be “calibrated” to convert them to calendar ages. de Vries also postulated that the fluctuations were due to the production of  $^{14}\text{C}$  and how it changed during variations in cosmic ray production. This brings us to two reasons why a radiocarbon date is not a true calendar age. The true half-life of  $^{14}\text{C}$  is 5,730 years and not the originally measured 5,568 years used in the radiocarbon age calculation, and the proportion of  $^{14}\text{C}$  in the atmosphere is not consistent through time. The latter is due in part to fluctuations in the cosmic ray flux into our atmosphere (e.g., sunspot activity). Since then there have been many studies examining the



**Radiocarbon ( $^{14}\text{C}$ ): Dating and Corals, Figure 1** Schematic of  $^{14}\text{C}$  production and decay in the atmosphere.  $^{14}\text{C}$  is produced in the atmosphere by cosmic neutrons colliding with Nitrogen atoms. The newly formed  $^{14}\text{C}$  is oxidized to  $^{14}\text{CO}_2$  where it then enters the biosphere. Following an organism's death, radioactive decay occurs converting the  $^{14}\text{C}$  back to  $^{14}\text{N}$ .

variations in the  $^{14}\text{C}$  production and its effects on the radiocarbon age to calendar age calibration (e.g., Stuiver, 1971; Edwards et al., 1993; Kitagawa and Van de Plicht, 1998; Stuiver et al., 1998; Fairbanks et al., 2005). The proportional amount of  $^{14}\text{C}$  to total carbon has also changed during the industrial revolution ( $\sim 1890$ ). Since fossil fuel is derived from millions of year old organic carbon, it contains no  $^{14}\text{C}$ . The burning of fossil fuels has caused a dilution of  $^{14}\text{C}$  in the atmosphere, this is the so-called Suess effect named after Hans Suess (Suess, 1965, 1980).

It is essential to have radiocarbon ages calibrated to calendar ages so as to have an accurate measure of time. It is also important to be able to compare ages with samples dated by other means, for example, uranium-series dating. It therefore became necessary to create a calibration between radiocarbon dates and calendar age. The ideal calibration material must have a precise calendar age and sample the atmosphere (carbon reservoir of interest).

### Tree-ring calibration

Fortunately, there is a suitable calibration material available in nature and this is called annual tree rings. Since those first measurements in the 1950s a detailed, precise calibration between radiocarbon and calendar age has been developed using many long-lived tree species. Dendrochronology provides the accurate calendar age for each ring in the tree, and then a radiocarbon age can be assigned to each calendar age. Several tree-ring chronologies have been constructed including the Belfast Irish Oak chronology (Baillie et al., 1983; Brown et al., 1986) back to  $\sim 7,200$  years and the Stuttgart–Hohenheim oak and pine chronology (e.g., Friedrich et al., 2004; Schaub et al., 2008; Hua et al., 2009) back to  $\sim 12,594$  years using thousands of accurately dated tree rings. However this is as far back in time as the continuous tree-ring radiocarbon calibration can be extended at present. More old trees are being discovered every year and this may eventually increase this calibration dataset at a later date. There are also a number of “floating” tree-ring chronologies that are being developed. They are called floating because they do not have a direct calendar age and must use the radiocarbon to match their ages. Many sections of old subfossil New Zealand Kauri trees have been found that span time from 25 to 60,000 years old (Hogg et al., 2006; Turney et al., 2007).

In order to extend the calibration curve back to 50,000 years other archives have been targeted, these include Foraminifera preserved in continuous annually laminated (varved) sediments (e.g., Kitagawa and van der Plicht, 2000; Hughen et al., 2004), tropical surface corals (e.g., Bard et al., 1998; Burr et al., 1996, 2009; Cutler et al., 2004; Fairbanks et al., 2005; Chiu et al., 2007), and speleothems (e.g., Beck et al., 2001; Genty et al., 1999). These additional archives extract their carbon from the dissolved inorganic carbon surrounding them and not directly from the atmosphere. But the carbon is closely linked to the atmosphere and can be corrected for this

offset. Both fossil corals and speleothems can be precisely dated to a calendar age by uranium-series dating and therefore can be used in extending the radiocarbon calibration curve. Beyond the tree-ring calibration, fossil corals and Foraminifera from Cariaco Basin and the Iberian Margin make up the calendar age to radiocarbon age calibration (Figure 2).

### Calibration curves

Over the last 20 or so years there have been several calibration “curves” ratified by the Radiocarbon International Community (IntCal98, IntCal04, IntCal09; Stuiver et al., 1998; Reimer et al., 2004; McCormac et al., 2004; Reimer et al., 2009), there have also been other calibration curves proposed by individual research groups (e.g., Fairbanks et al., 2005). Figure 2 shows the most recent IntCal09 calibration curve superimposed over many of the coral and foram varve archives. These calibration curves form the basis of several online calibration programs that take the radiocarbon age and output a calibrated age, the four major online calibration programs are the following:

Calib – <http://intcal.qub.ac.uk/calib/>

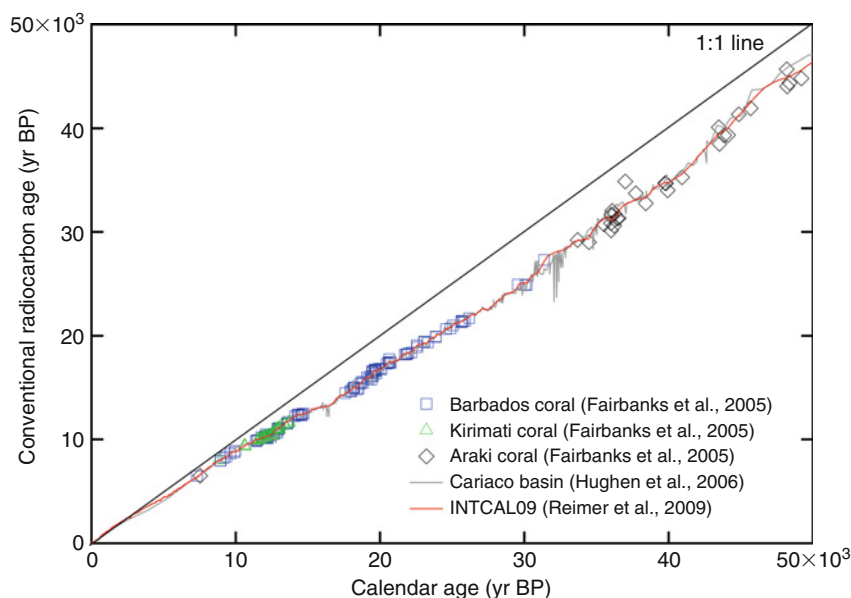
CalPal – <http://www.calpal.de/>

OxCal – <http://c14.arch.ox.ac.uk/embed.php?File=oxcal.html>

Fairbanks – <http://radiocarbon.ldeo.columbia.edu/research/radcarbcal.htm>

### Radiocarbon in the ocean

Marine organisms have a further complication when it comes to radiocarbon dating. The exchange between the ocean and atmospheric  $^{14}\text{CO}_2$  takes on average 10 years to come into equilibrium (Broecker et al., 1985), which never completely happens. Because the reservoir of carbon in the ocean is so vast and the mixing between the surface and deep ocean is sufficiently long, radioactive decay of carbon in the ocean occurs. The deep ocean can have an apparent age of several thousand years. This old carbon mixes upward by a process called “upwelling.” Amounts of upwelling vary throughout the oceans of the world. This results in the surface ocean having an average apparent age of  $\sim 400$  years although there is considerable variability. This is called the reservoir age or reservoir effect (e.g., Druffel et al., 2008; Eiriksson et al., 2004; Franke et al., 2008). Marine shells of known age collected prior to 1955 and independently dated corals have been used to measure this reservoir variability (e.g., Bourke and Hua, 2009; Cullen et al., 2006; Petchy et al., 2009). Online databases are available to estimate the reservoir age of a marine sample (Reimer and Reimer, 2009 <http://calib.org/marine>; Butzin et al., 2005; <http://radiocarbon.ldeo.columbia.edu/research/resage.htm>). This is then used to adjust the radiocarbon age and calibrate to a calendar age. A full marine calibration curve is also available (Marine04, Marine09) to calibrate a marine radiocarbon age, it was calculated using an ocean-atmosphere box



**Radiocarbon ( $^{14}\text{C}$ ): Dating and Corals, Figure 2** Radiocarbon calibration figure, conventional radiocarbon age on the y-axis vs. Calendar age on the x-axis. The IntCal09 dataset is used back to 50,000 years BP comprises tree-ring data, (Reimer et al., 2009, red line), corals from various locations can also be used to constrain this calibration. Shown here is corals data from Barbados (blue square), Kirimati (green triangle), and Araki (purple diamond) from Fairbanks et al. (2005). Also shown are Foraminifera from Cariaco Basin in the thin line (Hughen et al., 2006).

diffusion model for the time period 0–10,500 years (Oeschger et al., 1975; Stuiver and Braziunas, 1993) and foram and coral data from 10,500 to 12,500 years as described in Hughen et al. (2004). Beyond 12,500 years, the atmospheric calibration curve is used with a constant reservoir age of 405 years (Reimer et al., 2009).

#### “Bomb” radiocarbon

During the 1950s and 1960s, nuclear weapons testing generated excess neutrons in the atmosphere thereby creating manmade  $^{14}\text{C}$ . This production ceased in 1963 with the signing of the nuclear test ban treaty, however not before the  $^{14}\text{C}/\text{C}$  ratio in the atmosphere nearly doubled. This “bomb” radiocarbon has been used to help understand the uptake of  $\text{CO}_2$  by the ocean and by the terrestrial biosphere. The subsequent invasion of this “Bomb”  $^{14}\text{C}$  into the surface ocean has increased the radiocarbon difference between the surface and the deep ocean (e.g., Broecker, et al., 1985). The use of  $^{14}\text{C}$  as a global ocean circulation tracer was a primary objective of the study of the distribution of natural and bomb-produced  $^{14}\text{C}$  in the Geochemical Ocean Sections Study (GEOSECS) of the early 1970s (Ostlund and Stuiver, 1980; Broecker et al., 1985) and of the present-day World Ocean Circulation Experiment (WOCE; Key et al., 1996). The GEOSECS data identified a surface water gradient of post-bomb  $^{14}\text{C}$  from the equator toward the temperate latitudes. Broecker and Peng (1982) interpreted this distribution as representing

upwelling of low  $^{14}\text{C}$  water from the lower thermocline in equatorial regions, with migration of the  $^{14}\text{C}$  rich surface water toward higher latitudes.

Radiocarbon measurements of coral skeletal material have been used to study how the radiocarbon content of the tropical surface ocean has varied through time (e.g., Druffel 1981; Guilderson et al., 2000, 2009). Many coral genera construct massive colonies often 200–400 years old, which in shallow reef environments have growth rates on the order of  $1 \text{ cm year}^{-1}$ . Because the radiocarbon in the coral aragonite skeleton reflects seawater radiocarbon content at the time of deposition, radiocarbon measurements across annual skeletal density bands in such corals make it possible to reconstruct the annual mean radiocarbon content of the surface ocean back to pre-bomb and preindustrial values

#### Summary

Radiocarbon is a useful means for obtaining the age of death of a carbon-bearing organism. With the help of international scientists, a robust calibration has been developed back to 50,000 years ago. Annual tree rings provide the calibration back to  $\sim 12,594$  year BP and corals and forams helped refine this calibration back to 50,000 years ago using uranium-series dating in conjunction with radiocarbon dating. Corals have also played a role in trying to understand the oceanic uptake of  $\text{CO}_2$  and for tracking ocean currents and circulation.



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## Cross-references

[Uranium Series Dating](#)

## RECENT SEA LEVEL TRENDS

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## Synonyms

Sea level; Sea surface height; Still water level

## Definitions

**Sea level.** Height of the sea relative to the height of a benchmark on the nearby land (in tide gauge data analysis). Height of the sea relative to a reference surface such as an ellipsoid or geoid (in altimeter data analysis).

**Mean sea level.** Sea level averaged over a period of time, such as a month or year, long enough that fluctuations caused by waves and tides are largely removed (in tide gauge data analysis).

**Still water level.** The sea level that results from ocean processes including tides, surges, and mean sea level changes but not including waves.

**Sea surface height.** A term synonymous with “sea level” but used mostly in altimeter data analysis.

**Sea level trends.** Rates of change of sea level over a stated period either for a given location or averaged over a region or the global ocean.

## Introduction

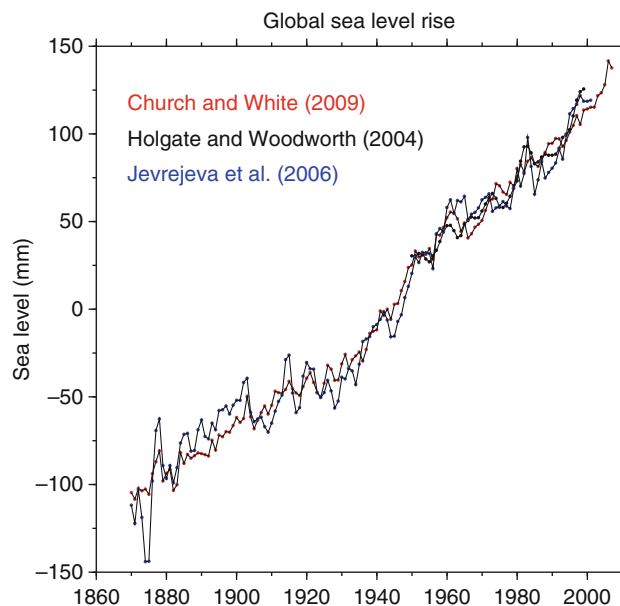
Sea levels have been measured with what are usually called “tide gauges” for many hundreds of years, both for practical purposes, such as efficient operation of a harbor, or for scientific research. For example, the first extended set of sea level measurements in the UK comprised heights and times of high water at Liverpool during 1764–1793 recorded by William Hutchinson (Woodworth, 1999). By the 1830s, the automatic tide gauge had been developed, consisting of a float in a stilling well and with the float’s motion recorded on a paper chart. The credit for this development is often given to Palmer following his installation of a gauge at Sheerness, UK in 1832 (Pugh, 1987). In the 1970s, the first satellite radar altimeters were launched. Altimeters record the propagation time of radar pulses transmitted

from the satellite, reflected off the ocean, and received back at the satellite. Sea levels can be measured by this means with an accuracy of several centimeters and on a near-global basis (Fu and Cazenave, 2001). This technique attained optimal reliability and accuracy with the deployment of the TOPEX/POSEIDON (T/P) mission in 1992. Since that time, the community has had near-continuous availability of precise altimeter data from T/P and JASON-1 and -2, complemented by data sets from the lower-flying ERS-1 and -2 and ENVISAT satellites. Tide gauges and altimeters have together demonstrated that sea levels change over many different temporal and spatial scales.

### Recent sea level trends

Since the last ice age around 20,000 years ago, mean sea level (MSL) has risen worldwide by more than 120 m. Over the last few millennia, the rate of rise has been no more than a few tenths of mm/year. However, an acceleration appears to have taken place between the eighteenth and nineteenth centuries and into the twentieth century, based on the small number of available long European tide gauge records (Woodworth, 1999; Jevrejeva et al., 2008) and on complementary data from salt marshes (e.g., Gehrels et al., 2006). A consensus has emerged that the twentieth century rise in global sea level was closer to 2 than 1 mm/year, with values around 1.7 mm/year having been obtained recently for the past century (Cazenave and Nerem, 2004; Church and White, 2006) or past half-century (Church et al., 2004; Holgate and Woodworth, 2004). However, the rate of change was far from constant, with an acceleration around 1920–1930, a deceleration after 1960, and a relatively recent acceleration in the late 1980s or early 1990s (e.g., Woodworth et al., 2009; Douglas, 2008; Merrifield et al., 2009). The high rate in the latter period of over 3 mm/year was observed not only by tide gauges but also by satellite altimetry (Beckley et al., 2007). It has been suggested this high rate may be connected partly with a sea level recovery that started in the mid-1980s following a sea level fall after the El Chichón volcanic eruption (Domingues et al., 2008).

Figure 1 presents findings on global sea level rise by different authors, and there is general agreement between them. However, it must always be kept in mind that our knowledge of recent change is based largely on a sparse data set, that of the Permanent Service for Mean Sea Level (PSMSL) (Woodworth and Player, 2003), and that there can be considerable spatial and temporal variability in sea level change (cf. Figure 1 of Wunsch et al., 2007 for a demonstration of spatial variability in trends since the early 1990s). Sea level time series at particular locations, including coral islands, can be found in individual reports (e.g., Woodworth, 2005) and from the PSMSL web site [www.psmsl.org](http://www.psmsl.org). Vertical land movements (VLMs) due to glacial isostatic adjustment (GIA), tectonic or anthropogenic processes can play important roles in the sea level changes observed by tide gauges and by other in situ



**Recent Sea Level Trends, Figure 1** Global sea levels from three recent studies, all based on MSL data from the PSMSL. Note the higher rates of rise after 1930 and in recent years. Values denoted Church and White (2009) are updated from those reported in Church and White (2006).

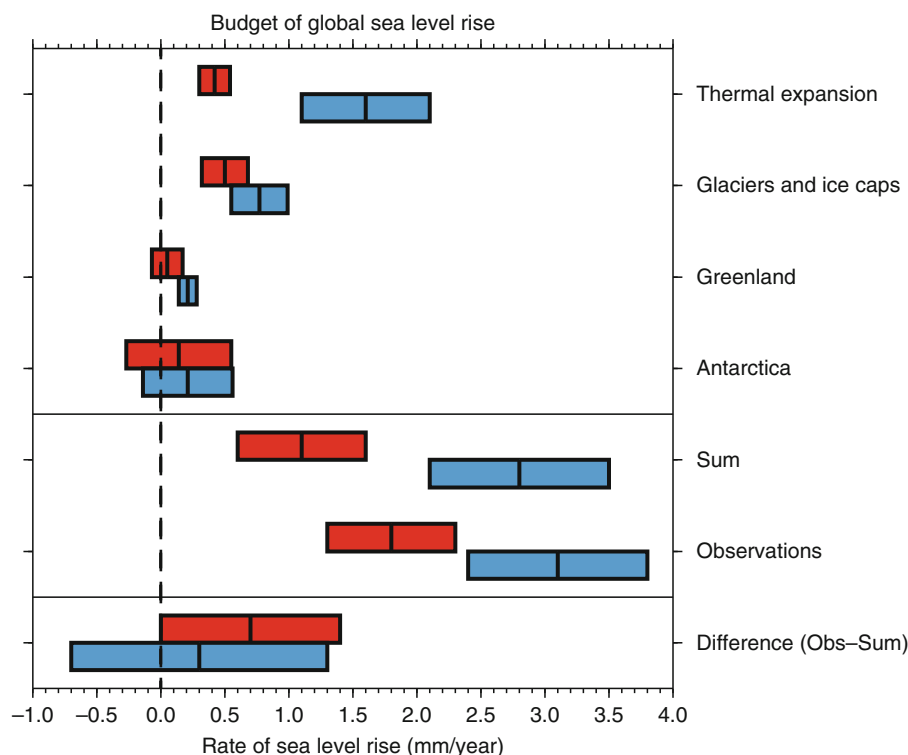
techniques. VLMs due to GIA can be estimated with the use of geodynamic models (e.g., Peltier, 2001), while advanced geodetic techniques (notably Global Positioning System and Absolute Gravity) are being developed to monitor VLMs, of whatever origin, at tide gauge sites (Woodworth, 2006).

### Understanding the observed sea level rise

MSL is often described as an “integral parameter”, providing an integration of sea level changes resulting from many climate-change related processes over many years, of which oceanic thermal expansion, melting of glaciers, ice caps and ice sheets, and modifications to hydrological exchanges between land and ocean are the most important. Consequently, if MSL is changing, it points to major changes in one or more of the climate-related drivers of that change. Ice sheets have the potential to raise sea level by far more than the other processes (see Table 11.3 of Church et al., 2001), although their contribution during the past century appears to have been small.

The composition of the various contributions to sea level change (the “sea level budget”) forms a major research topic which is addressed regularly in the scientific assessments of the Intergovernmental Panel on Climate Change (IPCC), the most recent being the Third Assessment Report (TAR) (Church et al., 2001) and Fourth Assessment Report (AR4) (Bindoff et al., 2007). Figure 2 summarizes the budget calculated by the AR4. The inability of these assessments to account for most of the observed rise (the “sea level enigma” of





**Recent Sea Level Trends, Figure 2** Contributions to sea level rise (upper four entries), their sum, and the observed rates of sea level rise for 1961–2003 (red) and 1993–2003 (blue). The bars represent the uncertainty range. The difference (Obs – Sum) represents the “sea level enigma.” For details, see Bindoff et al. (2007).

Munk, 2002) has to some extent been resolved, at least for recent decades, by a reworking of hydrographic data sets and through the availability of more complete space and in situ instrumentation for the determination of thermal expansion (Domingues et al., 2008). At the time of writing, “budget estimates” for the last decade, during which the community has had available information from satellite gravity [i.e., the Gravity Recovery And Climate Experiment (GRACE) mission] and Argo hydrography in addition to altimeter and tide gauge data, have been more consistent, although discrepancies remain (Willis et al., 2008; Cazenave et al., 2009). One is confident that consensus will eventually be achieved as global observation systems become more complete.

Reviews of the field have been undertaken by individual scientists (e.g., Cazenave and Nerem, 2004; Woodworth, 2006) and national and international study groups in between the IPCC assessments. One such major review of the status of research was undertaken by the World Climate Research Program (WCRP) in 2006 (Church et al., 2007) from which full reports on each sector of the field will be published in book form in 2010 (Church et al., 2010). One chapter is concerned with the use of sea level information derived from coral reefs, in addition to salt marsh and other coastal geological data, as a complement to and extension back in time of the instrumental record (Lambeck et al., 2010).

### Changes in extreme sea levels

As extreme sea level events often result in flooding and loss of life, an important question is whether their amplitudes and frequencies are changing, and if the levels of extreme high waters are changing in a significantly different way to MSLs. The only study which has attempted a quasi-global investigation of this topic is that of Woodworth and Blackman (2004) who studied data from 141 stations, and concluded that there is indeed evidence for an increase in extreme high water levels worldwide since 1975, as reported frequently in the press. However, in most cases, the secular changes and the interannual variability in the extremes were found to be similar to those in MSL. A number of other studies of sea level extremes at particular locations are available, although as they are for different epochs and use different methods, it is difficult to arrive at general conclusions. A review of these studies and of the meteorological forcing factors which result in extreme levels has been provided by Lowe et al. (2010).

### Predictions of future sea level trends

The IPCC assessments also provide regular updates on future sea level rise predictions based on climate modeling. The TAR projected a global averaged sea level rise of between 20 and 70 cm between 1990 and 2100 using

the full range of IPCC greenhouse gas scenarios and a range of climate models. When an additional uncertainty for land-ice changes was included, the full range of projected sea level rise was 9–88 cm. For the IPCC AR4 (Meehl et al., 2007), the range of sea level projections using a larger range of models was 18–59 cm (90% confidence limits) over the period from 1980–1999 to 2090–2099. The largest contribution was from ocean thermal expansion with the next largest contribution from glaciers and ice caps. However, there is increasing concern about the stability of ice sheets, and recognizing this deficiency, the AR4 increased the upper limit of the projected sea level rise by 10–20 cm, implying an overall range of projected sea level rise of 18–79 cm. It is unclear what confidence intervals to assign to this range given the ice sheet uncertainties. Note that they also stated that “larger values cannot be excluded, but understanding of these effects is too limited to assess their likelihood or provide a best estimate or an upper bound for sea level rise.”

While the 2001 and 2007 IPCC projections are somewhat different in how they treat ice sheet uncertainties and the confidence limits quoted, a comparison of the projections (Figure 6 of Church et al., 2008) shows the end results are similar, except that the lower limit of the 2001 projections has been raised from 9 cm in the TAR to 18 cm in the AR4.

Despite the additional allowance for ice sheet uncertainties, a number of scientists remain concerned that the ice-sheet contributions in the AR4 may have been underestimated, and they adopt a more phenomenological approach to estimating future sea level rise. For example, Rahmstorf (2007) developed a simple statistical model that related twentieth century surface temperature change to twentieth century sea level change. Using this relationship and projected surface temperature increases, he estimated that twenty-first century sea level rise might exceed the IPCC projections and be as much as 1.4 m. Holgate et al. (2007) raised concerns that Rahmstorf’s model is too simplistic and may not adequately represent future change. Similar conclusions, that the AR4 sea level rise predictions may have been underestimated have been based on analysis of longer term temperature and sea level information (Grinsted et al., 2009). One remains concerned at the low physics content of some of these parameterizations. Nevertheless, the concern that the IPCC sea level projections may be biased low has been reinforced by a comparison of observed and projected sea level rise from 1990 to the present. For this period, observed sea level has been rising at the very upper end of the IPCC TAR projections (Holgate and Woodworth, 2004; Rahmstorf et al., 2007), indicating once more that one or more of the model contributions to sea level rise may be underestimated.

Future IPCC assessments are likely to pay greater attention to regional changes in MSL, as opposed to global-average ones, and include in impact studies the role of regional land movements. In addition, they will study in more detail changes in climate extremes (extreme sea

levels leading to coastal flooding in this case) as well as in climate means (MSL in this case). For example, the decimetric twentieth century sea level rise has already doubled the risk of flooding since 1901 at many locations around the UK coastline. If sea level rises faster in the twenty-first century, as suggested by the AR4, there will be greater risk to the coastal environment and infrastructure. In addition, climate-related changes in regional wind fields will result in changes in storm surge frequency and magnitude which will modify the changes in risk due to MSL rise alone (Woodworth et al., 2007; Lowe et al., 2010).

### Need for ongoing monitoring of sea level

Descriptions of global and national sea level networks and their data sets can be found at the web sites of the PSMSL and the Global Sea Level Observing System (GLOSS, [www.gloss-sealevel.org](http://www.gloss-sealevel.org)), while methods for monitoring sea level are explained in the PSMSL training web pages. Real-time data provision, in addition to the delayed-mode data needed for scientific research, is increasingly encouraged for two reasons: the data are then available to a wide range of new users in “operational oceanography” including coastal protection; and faults can be identified faster, leading to better delayed mode data sets in the long term. Some sea level stations are now “multi-hazard” sites, with sensors specifically designed for the high rate recording needed for tsunami monitoring. It is clear that the world needs a coordinated and complete sea level monitoring network at global, regional, and local scales, including information both from in situ sources and from a range of space-based instrumentation (notably altimetry and space gravity, Wilson et al., 2010).

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## Cross-references

[Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity](#)  
[Sea Level Change and Its Effect on Reef Growth](#)  
[Sea-Level Indicators](#)



## RED SEA AND GULF OF AQABA

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### Definition

The Red Sea is a narrow elongated water body extending some 2,000 km SE–NW, between latitudes 16°N and 28°N, from the Gulf of Aden through which it connects from the Gulf of Aden (through which it connects to the Indian Ocean) to the Gulf of Aqaba (Figure 1). It is flanked by east Africa (Egypt, Sudan, Eritrea, and Djibuti) to the west and Arabia (Saudi Arabia and Yemen) to the east. The Red Sea hosts spectacular coral reefs that pertain to the Indo-Pacific domain. Its northern tributaries, the Gulfs of Suez and Aqaba (reaching latitude 29.5°N) are home to some of the northernmost coral reefs in the world.



**Red Sea And Gulf Of Aqaba, Figure 1** Satellite image of the Red Sea and its northern tributaries, the Gulfs of Suez and Aqaba.

## Red Sea coral reefs – geology and ecology

### Setting

An incipient oceanic basin separating the African Plate from the Arabian Plate, the Red Sea was born as an extensional basin during the late Oligocene – early Miocene, with actual sea floor formation occurring since about 5 million years ago at its southern part. The Red Sea is connected to the Indian Ocean by way of the shallow and narrow sill of Bab-el-Mandeb (137 m deep and 29 km wide) and the Gulf of Aden.

From its southern end at Bab-el-Mandeb, the Red Sea extends nearly 2,000 km until it diverges into two smaller gulfs, the Gulf of Suez and the Gulf of Aqaba. This junction connects the mostly extensional Red Sea with the abandoned rift of the Gulf of Suez and the mostly left-lateral Dead Sea transform of which the Gulf of Aqaba is an active part. Rifting processes resulted in block tilting and an asymmetrical bathymetry across the Red Sea. The Egyptian–Sudanese (western) margin is steep with a narrow shelf and deep pull-apart basins floored by oceanic crust, whereas the Arabian (eastern) margin is less steep and floored by attenuated continental crust. The Red Sea proper is up to 350 km wide and has a maximum depth of 2,800 m, but its average depth is only ~450 m, since around 40% of the Red Sea is shallower than 100 m. The Gulf of Suez is about 320 km long and 70 km wide, with a maximum depth of less than 100 m, while the Gulf of Aqaba is 180 km long and up to 25 km wide with an average depth of 900 m and a maximum depth of nearly 1,850 m.

The margins of the sea on land form elevated shoulders reaching up to 3,000–4,000 m, a few tens of kilometers away from the shore. The coasts are generally narrow, with little or no coastal plain, and sandy beaches are found only in the vicinity of creek valley outlets. The Red Sea is surrounded by deserts and evaporation greatly exceeds precipitation. Freshwater input from the continent is limited to occasional flash floods.

### Reefs – morphology, distribution, and description

Warm temperatures and little runoff support reef growth, and active tectonics create steep margins that are often coral-covered to a depth of several dozen meters. On shallower slopes and wider margins, shallow reef shoals and a few coral islands develop.

Fringing reefs are the most common form of coral terraces along the coasts of the Red Sea (Head, 1987), but some patch reefs and coral islands also occur, especially off the Sudanese coast and the southern parts of both the western and eastern coasts. In general, reefs are better developed along the northern part of the Red Sea down to about latitude 18–20°N (Behairy et al., 1992), although coral growth rates were found to be higher in the south, decreasing northwards (Schuhmacher et al., 1995). To the south, sandy beaches become increasingly abundant and mangroves occupy parts of the coasts. At the southern parts of the Red Sea, reefs of coralline algae are also found

(Behairy et al., 1992). Fringing reefs on the northern parts of the Red Sea are generally narrow, being limited by the steep coastal margins, and form deep “walls”. To the south, the coastal plain is wider and the margins are less steep, allowing the development of wider lagoons and reefs further from shore. Patch reefs somewhat removed from the shores may form chains resembling barrier reefs. Along the coast from Al-Wadj south to Jeddah (eastern shore), a long chain of patch reefs was called the “Little Barrier Reef” by Sheppard (1985). Further south, groups of coral-supporting islands are found on both sides of the sea – the Dahlak and Farasan archipelagoes off the coast of Eritrea and Saudi Arabia, respectively. Some of the reefs growing on wide shallow carbonate platforms in the central and southern parts of the Red Sea have a circular shape enclosing a lagoon, thus resembling Pacific atolls. The best studied of these is perhaps Sanganeb Atoll, off Port Sudan (Schuhmacher and Mergner, 1985; Mergner and Schuhmacher, 1985; Reinicke et al., 2003). Many of the modern coral reefs along the Red Sea grow over fossil Pleistocene reefs.

Fringing coral reefs are also the overwhelmingly dominant form along the shores of the Gulfs of Suez and Aqaba, where the former are smaller and less developed than the latter. The difference may be due to the low winter temperatures at the shallow Gulf of Suez. At greater depths, down to at least 65–70 m, coral carpets covering marginal slopes are abundant. Growth of these deep reefs is facilitated by the clarity of the water that allows light penetration to a depth of ~100 m.

### Geological history of coral reefs at the Red Sea

Coral reefs seem to have been intermittently present along the shores of the Red Sea since Miocene times, persisting during periods in which good connection with the open ocean was maintained. Connection of the Red Sea with the Mediterranean finally ceased during the Pliocene, and from that period Indo-Pacific flora and fauna were introduced (Braithwaite, 1987). During glacial periods, the combination of low temperatures, high evaporation, and restricted water passage over the shallow sill at Bab-el-Mandeb due to low sea level possibly prevented the development of coral reefs. Conditions at the northern Red Sea and Gulf of Aqaba during the last glacial maximum are estimated at 4–5°C lower than present-day temperatures and salinity in the range of 50–53‰ (Arz et al., 2003; Siddall et al., 2003; Almogi-Labin et al., 2008).

Fossil Pleistocene coral reefs are found along the Red Sea coasts on both sides, off of Sudan and Saudi Arabia. These reach an elevation of at least 16 m above current sea level. Raised fossil coral reefs are also present at the Gulfs of Suez and Aqaba, with terraces at the Gulf of Aqaba, dating as far back as 300 ka, reaching some 35 m above sea level (Figures 2, 3; Gvirtzman et al., 1992). Fossil sequences of 3–4 reef complexes are found along the southern coast of Sinai and at the northeastern end of the Gulf of Aqaba, just south of the city Aqaba (Friedman, 1968; Gvirtzman et al., 1992; Al-Rifaiy and Cherif, 1988). The elevated Pleistocene sequences seem to represent Pleistocene highstands, reaching their present elevation as a result of uplifting tectonic movements along



**Red Sea And Gulf Of Aqaba, Figure 2** Uplifted fossil Pleistocene coral reefs covered by beach rock some 20 m above the sea. South of Aqaba, on the northeastern side of the Gulf of Aqaba. (Photo courtesy by Y. Shaked.)



**Red Sea And Gulf Of Aqaba, Figure 3** Fossil corals comprising uplifted Pleistocene reefs south of Aqaba. (Photo courtesy by Y. Shaked.)

those margins of the Gulf. On Tiran island at the entrance to the Gulf of Aqaba, where uplifting tectonics have particularly high rates, marine coastal terraces are found up to 500 m above the present-day sea level. Fossilized late Pleistocene fringing reefs are recognized to an elevation of 60 m above sea level, where an age of 146 ka was determined from a terrace at 40 m (Goldberg and Beyth, 1991).

Submerged terraces, such as those found at ~120 and 65–70 m depth along the northwestern end of the Gulf of Aqaba (Makovsky et al., 2008), likely represent lower sea level stand-stills. A reliable age control of these submerged features is not yet available. Since conditions at the Red Sea and its subsidiary gulfs were not favorable to reef formation during glacial periods, it seems that most modern reefs were established during the Holocene (Braithwaite, 1987). A coral from a fossil reef retrieved from 11 m below sea level yielded an age of 7,000 years (Shaked et al., 2004). Slightly exposed reefs along both margins of the Gulf of Aqaba indicate a sustained (ca. 7–4 ka) Holocene sea level highstand, ~1 m above present sea level. During this interval Holocene fringing reefs developed morphological reef flats that are now found at or just above the high-tide level, commonly partly eroded and covered with beach rock (Shaked et al., 2004, 2005). The modern reefs are found further offshore and are limited by the present sea level.

#### Present conditions

The Red Sea's deep, elongated morphology coupled with its location within a hyper arid region create a distinct anti-estuarine circulation at Bab-el-Mandeb, where relatively warm water (25.5–30°C) with normal salinity (36.5%) enters the Red Sea from the Gulf of Aden, forming the

surface water layer that cools and evaporates along the route northward. The Red Sea bottom water (21.7°C, 40.6%) is formed mostly in the Gulf of Aqaba (Plähn et al., 2002), flowing into the Red Sea over the shallow (250 m) and narrow (16 km) sill in the Straits of Tiran.

The presence of a shallow sill at Bab-el-Mandeb greatly affects the extent and diversity of the coral reefs in the Red Sea, especially those at higher latitudes in the Gulfs of Aqaba and Suez. Unlike “normal” open oceans, where the deep and intermediate water is cold, the shallow sill at Bab-el-Mandeb effectively separates the deep waters in the semi-enclosed Red Sea from those of the Indian Ocean. For example, the water at 1,500 m depth in the Gulf of Aden (the water body connecting the Red Sea to the Indian Ocean) is <10°C, whereas the deep waters at this and greater depths in the Red Sea is always warmer than 20°C. This characteristic determines the lowest temperature the shallow water can be cooled down to during winter. The ensuing year-round occurrence of warm waters allows coral reefs to flourish throughout the Red Sea, even at the northernmost end of the Gulf of Aqaba.

On the other hand, the occurrence of warm water at depth substantially weakens vertical stratification. For example, below ~300 m, the vertical gradient in temperature in the Gulf of Aqaba is ~0.09°C/100 m, compared with more than an order of magnitude steeper gradient in “normal” oceans at similar latitudes (e.g., 1.07°C/100 m south of Bermuda, 1.67°C/100 m at the Central North Pacific). The weak stratification in the Gulf of Aqaba, together with low air temperature during winter, drives an extraordinarily deep vertical mixing, exceeding 600 m depth in cold winters. The most striking phenomenon driven by this mixing is the recurrence of immense spring blooms of benthic algae that cover wide sections



of the local reefs, sometimes causing substantial coral death (Genin et al., 1995). This “intermediate” disturbance, occurring once every 5–20 years, may be one of the processes responsible for the high coral diversity in the Gulf (Connell, 1978). Note, however, that the occurrence of deep mixing is limited to the Gulf of Aqaba, at the northern end of the Red Sea. Air temperature at lower latitudes, south of the Straits of Tiran, is too high even in winters to induce deep mixing (Paldor and Anati, 1979; Reiss and Hottinger, 1984).

### Modern fauna

While its connection with the Indian Ocean places the biogeographic origin of Red Sea fauna and flora within the Indo-Pacific domain, its setting and geological history make for unique conditions that have direct bearing on the development of reefs along the coasts of this elongated narrow sea. The reefs are dominated by stony, hermatypic corals, consisting of a diverse mixture of branching, foliose, and massive species. Most abundant are corals belonging to the genera *Acropora*, *Stylophora*, *Montipora*, *Pocillopora*, *Porites*, *Platygyra*, *Pavona*, *Echinopora*, and *Favia* (Loya and Slobodkin, 1971). The hydrozoan *Millepora* is very abundant in the shallow, sub-tidal zone. Soft corals are also abundant throughout the Red Sea, dominated by *Sinularia*, *Sarcophyton*, *Lobophyton*, and Xeniids, with magnificent thickets of nephtheids (mostly *Dendronephthya*) found on elevated substrates and vertical walls exposed to strong currents (Benayahu and Loya, 1977). Due to the clear water in the northern Red Sea, zooxanthellate corals reach at least 145 m in depth (Fricke et al., 1987).

The number of coral species found in the Red Sea is approximately 190, belonging to 70 genera (Head, 1987). While the total number of species is generally higher in other tropical Indo-Pacific reefs (e.g., ~360 species in the Great Barrier Reef, Veron, 1986), the local, within-habitat diversity in the Red Sea is exceptionally high, even higher than in the Great Barrier Reef of Australia (Loya, 1972).

The fishes in Red Sea coral reefs, like the corals themselves, share an Indo-Pacific origin. Especially abundant and diverse are the lush guild of site-attached and mobile zooplanktivorous species (Figure 4), including many Damselfishes (Pomacentridae) and the most conspicuous schools of Reef Anthias, and numerous benthic feeding fishes, including Surgeonfishes (Acanthuridae), Parrotfishes (Scaridae), Wrasses (Labridae), Groupers (Serranidae), Butterflyfishes (Chaetodontidae), Triggerfishes (Balistidae), Blennies, and Gobies. Of the 462 reef-associated species that inhabit the Arabian Sea, 69% have crossed successfully into the Red Sea; of these, 55% have crossed into the Gulf of Aqaba. Present-day differences in the species richness of reef-associated species among the Arabian Sea, Red Sea, and Gulf of Aqaba appear to be the product of external, non-selective constraints on colonization (Kiflawi et al., 2006).

The Red Sea coral reefs are among the most studied reefs in the world. Detailed accounts of their structure and biological composition can be found in numerous publications. Some of the useful references include Loya (1972), Loya and Slobodkin (1971), Mergner (1971), Scheer (1971), Fishelson (1971), Benayahu and Loya (1977), and Edwards and Head (1987).



**Red Sea And Gulf Of Aqaba, Figure 4** A typical coral reef near Tiran, the passage between Red Sea and Gulf of Aqaba. (Photo courtesy by A. Genin.)

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## Cross-references

[Algae-Macro](#)  
[Atolls](#)  
[Barrier Reef \(Ribbon Reef\)](#)  
[Beach Rock](#)  
[Coral Reef, Definition](#)  
[Corals: Environmental Controls on Growth](#)  
[Earthquakes and Emergence or Submergence of Coral Reefs](#)  
[Emergent Reefs](#)  
[Fringing Reefs](#)  
[Great Barrier Reef Committee](#)  
[Holocene Reefs: Thickness and Characteristics](#)  
[Last Glacial Interstadials](#)  
[Last Glacial Lowstand and Shelf Exposure](#)  
[Last Interglacial and Reef Development](#)  
[Sea Level Change and Its Effect on Reef Growth](#)  
[Uranium Series Dating](#)

## REEF BALLS

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### Definition

**Artificial Reef:** Any manmade structure deposited or attached to the seafloor whether intentional or unintentional, which provides, or attempts to provide a substitute for some of the ecological services provided by natural reefs (e.g., shipwrecks, oil rigs, dumped construction debris, designed/purpose built modules).

**Designed Artificial Reef:** Any manmade structure purposely built and deployed with the intent of serving as an artificial reef (rather than repurposed).

**Breakwater:** A shallow submerged structure positioned in a nearshore high energy environment which absorbs some of the incoming wave energy, reducing the impact on the beach.

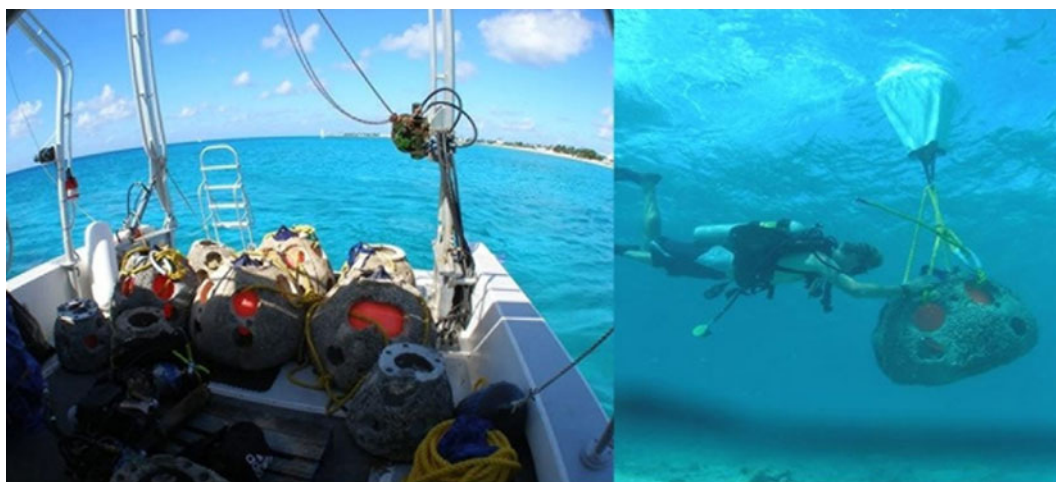
**Mitigation:** Human activity intended to compensate for damage done to an ecosystem by a natural or anthropogenic impact (e.g., hurricane, ship grounding, dredging, etc. . .).

**Anthropogenic:** Caused by human activity.

Reef Balls™ are hollow concrete hemispherical designed artificial reef modules built by The Reef Ball Foundation and its licensees, ranging in size from about 13kg (30lbs) to over 4 metric tons (8800 lbs) (<http://www.reefball.org/technicalspecs.htm>). While the term “Reef Ball” is often used incorrectly to describe any of a number of roughly hemispherical artificial reef designs, true Reef Balls possess a number of unique adaptations for a wide range of designed artificial reef applications (Figure 1). Reef Balls utilize a pH balanced microsilicate based concrete

mixture, which is textured to promote natural settlement for hard and soft corals (see also *Corals: Environmental Controls on Growth*). They may also be fit with adapters for coral transplant and rescue operations (Quinn et al., 1999; Bowden-Kerby, 2003), or be anchored for use as a breakwater (e.g., Harris, 2003) (see also *Waves and Wave-Driven Currents*). The shape of a Reef Ball makes it extremely stable, and able to withstand strong hurricane waves when properly engineered and deployed (Harris, 2003; Armonio, 2004). Exclusion of metal components gives Reef Balls an expected lifespan of 500+ years in seawater (ASTM, 2008), an important consideration in the rehabilitation of coral reefs, which are very slow growing (see also *Reef Restoration*).

Artificial reefs have been increasingly utilized for habitat rehabilitation and mitigation of anthropogenic impact (e.g., Pratt, 1994; Pickering et al., 1998, see Chapters *Reef Restoration*, *Reefs at Risk: Map-Based Analyses of Threats to Coral Reefs*) (Figure 2), but the degree to which artificial reefs can accomplish these goals is still a topic of scientific scrutiny (e.g., Osenberg et al., 2002; Baine, 2001; Powers et al., 2003). However research shows that artificial reef units with higher levels of habitat complexity and void space are capable of supporting more biomass and diversity of fish per square meter of restored area (Charbonnel et al., 2002; Sherman et al., 2002), and that artificial reefs which better approximate natural habitat can more closely approximate the natural fish and invertebrate communities (Perkol-Finkel et al., 2006) (Figure 3). This research tends to support the use of designed artificial reef units (such as Reef Balls) over other traditional artificial reef building materials (typically materials of opportunity, such as concrete rubble, ash blocks, tires, or construction debris which less closely replicate natural habitat). It is important to note, however, that no



**Reef Balls, Figure 1** Reef Balls staged on a boat awaiting deployment (left). Note the small circular adaptor holes on the tops and sides of the balls, used for transplant of coral fragments. The removable central air bladder allows units to be easily deployed and positioned by divers (right) when working in the vicinity of live corals. Photo credit: <http://www.reefball.org>.



form of restoration or mitigation can equal the ecosystem services provided by the natural habitat, so the best form of restoration is always conservation (e.g., Young, 2000) (see also *Conservation and Marine Protected Areas*).

The successful use of Reef Balls has been scientifically documented for project goals ranging from breakwaters

and erosional stability (Harris, 2003), to oyster culture (Wall et al., 2005) and mangrove restoration (Krumholz and Jadot, 2009). However, despite extensive use in fisheries augmentation coral rescue, and mitigation (e.g., Edwards and Gomez, 2007; Bowden-Kerby, 2003), the ability of designed artificial reefs to succeed in these roles



**Reef Balls, Figure 2** Newly deployed Reef Balls in a breakwater formation in Grand Cayman, BWI. Submerged Reef Ball breakwaters offer a softer more porous approach, providing many of the benefits of traditional beach hardening techniques while also providing habitat for fish and invertebrates. Photo credit: <http://www.reefball.org>.



**Reef Balls, Figure 3** A reef Ball in Indonesia which has been in place for about 5 years. This reef ball has a few transplanted corals as well as several species of naturally recruited hard and soft corals covering virtually 100% of its exposed surface area after only a few years in the water. Photo credit: <http://www.reefball.org>.

has yet to be systematically evaluated (e.g., Osenberg et al., 2002; Baine, 2001; Powers et al., 2003).

Since its inception in 1993, the Reef Ball Foundation has implemented or overseen the placement of over 500,000 Reef Balls in about 4000 projects in 60+ countries. The Foundation's mission is to help restore the world's ocean ecosystems through the development and use of aesthetically pleasing, ecologically sound, and economically designed artificial reefs, emphasizing on-going research, public education, community involvement, and reefs that promote and support natural species diversity and population density.

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## Cross-references

[Conservation and Marine Protection Areas](#)

[Reef Restoration](#)

[Reefs at Risk: Map-Based Analyses of Threats to Coral Reefs](#)

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## REEF CLASSIFICATION BY FAIRBRIDGE (1950)

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## Introduction

Coral reefs have been the subject of scientific interest for the last century and a half, with Darwin's (1842) descriptions of the basic reef forms (i.e., fringing, barrier, and atoll reefs) still in common use today. In the Australian Indo-Pacific region, originally Fairbridge (1950) mainly focused on the Great Barrier Reef (GBR) in broad outline but later elaborated and extended his system to more comprehensively include the whole of the Australian region (Fairbridge, 1967), covering in more detail reefs on the west coast continental platform along western and north-western Western Australia as well as those reefs occurring along the northern margins of the continent offshore the Northern Territory and northern Queensland in the Arafura Sea and Torres Strait.

The Fairbridge classification of Holocene and Pleistocene reefs is comprehensive in that it covers the salient morphological reef forms on the relatively stable epicontinental Australian shelf environment. He recognized fringing, barrier, atoll, and platform reefs along with five varieties of coral island. This basic classification was initially modified and expanded by Maxwell (1968), and then subsequently more comprehensively described by Hopley (1982) and Hopley et al. (2007). Fairbridge's first description in the *Journal of Geology* (Volume 58, pp. 330–401), about 70 pages long, was based in part on Rhodes' exposure to the photo-interpretation of coral reefs during World War II. This fortuitous occurrence is noted by Hopley et al. (2007), who state that:

"...Fairbridge was possibly the first person with a geoscientific background to view the variety of reefs, the planimetric details of which had not been previously seen. Such a view gives new insight into the role of waves and currents in the formation of reefs whilst the appreciation of the range of morphology led for the first time to an evolutionary type of classification of modern reefs." (p. 12).

Using his geoscientific background based on interpretation of reef borings and structural and geomorphological features, Fairbridge posited that the shape of coral reefs is generally controlled by wind, waves, and currents but complex forms could also be influenced by antecedent bottom topography, sedimentation, and eustatic fluctuations.

As far as reef types are concerned, almost all of the “standard” forms are known to occur in the region, based mostly on observations of the GBR which extends over 19,300 km along the Queensland coast (Fairbridge, 1950). Most common in the region are irregularly shaped reefs, which do not fit into any standard category – the platform or patch reefs, which are also alternatively referred to as bank or hummock reefs (Fairbridge, 1950, page 332). Atolls are rare on the Australian shelf but were reported to occur sporadically off the northwestern coast and on the Queensland shelf. At this time, fringing reefs were recognized as being common in the north but it is now widely recognized that Australia’s largest fringing reef occurs on the West Australian shelf (Collins et al., 2003). Ningaloo Reef, located about 1,200 km north of Perth, is 300 km long and it is also the world’s only large reef located so close to a landmass. At its point closest to the continent, the reef is just 100 m from shore; at its farthest point, it is less than 7 km away.

### Fringing reefs

As summarized by Kennedy and Woodroffe (2002), it is now known that fringing reefs grow along the shore under a great variety of conditions that are imposed by climate, vegetation, soils and sediments, and rock materials of the adjacent land mass. Several decades ago, Fairbridge (1950) noted that fringing reefs of the Australian mainland are among the poorest of reef types due to rigorous conditions near the shore, excessive sedimentation, dilution of seawater by fresh water, and acidic waters from the land. More vigorous fringing reefs often encircle offshore continental islands where growth conditions are more favorable. Smithers et al. (2006) have additionally shown that fringing reefs of the GBR have experienced several critical growth phases since the mid-Holocene. They report that the apparent synchronicity of these growth-and-quiescent phases over wide geographical areas are related to the involvement of broad-scale influences such as climate and sea-level change. But, in general, as observed by Fairbridge long ago, (episodic) living coral growth is confined to the outer reef edge, where there may be a *Lithothamnion* ridge, whereas behind it there is a dead reef, about a meter below low-water springs, lightly sand covered and marked by the radial pattern of seaweed. The reef flats often contain coral shingle, and living coral is absent except in tide pools. Landward-most parts of some fringing reefs are characterized by mud-covered reef that is in the process of colonization by mangrove. Morphological zonation often follows an outer to inner reef pattern of reef edge, trickle zone, sand flat mangrove. Good examples occur in the Whitsunday Group, the

Lizard Islands, and the Murray Islands off the Queensland coast (Fairbridge, 1967). The geographic distribution of coral reef types in the Australian region is shown in Figure 10 of Fairbridge (1950). Figure 17.4 of Fairbridge (1967) details locations of reef types of the GBR, Coral Sea, and southeastern Papua New Guinea. Figure 17.8 in the same publication shows shelf regions around the Australian island continent as well as some other prominent geographic features relevant to the study of coral reefs.

### Barrier reefs

Fairbridge (1950) states that the only barrier reefs in Australia are the outermost belt of the Queensland reefs. Barrier reefs are always strongly asymmetric in planview and cross-section, being steep on the ocean side and grading towards the land with a sediment wedge dotted by small reef patches, pinnacles, and coral heads (Fairbridge, 1967). Incipient barriers may include small fringing reefs around islands within the main lagoon, such as Lizard Island. Discontinuous reefs near the edge of the Sahul Shelf may be genetically linked to the barrier type, but from a morphological point of view they are only patch or platform reefs, as described by Fairbridge and Teichert (1948). Fairbridge (1967) states that the world’s best example of a barrier reef system occurs along the Queensland coast from the Gulf of Papua to the Tropic of Capricorn, a distance of 1,900 km. In his 1950 classification, Fairbridge recognized two main types of outer-barrier reefs: ribbon reefs and platform reefs.

The **ribbon-reef zone**, containing ribbon-shaped reefs (the ‘linear reefs’ of Jukes, 1847), occurs as a festoon along the outer edge of the continental shelf. Here, the ribbon reef ranges between 300 and 450 m in width and 3–25 km in length. The ribbons are separated from one another by narrow passages generally about a kilometer wide. Typical of this type and extensively studied is the Yonge Reef east of Lizard Island. This ribbon reef consists of an outer parapet-like fringe of living corals that are furrowed by wedge-shaped channels or chutes. Inside the margin, there is a shallow zone or outer moat, which is occupied by irregular patches of living coral, negroheads, and boulders that are heavily washed by surf. The reef crest rises gently from here, often including a *Lithothamnion* rim of calcareous algae about 1–2 m above low-water springs. The reef material consists of debris containing broken corals, boulders, shells, and sand, cemented together and often encrusted by *Lithothamnion*. The so-called “trickle zone” or “radial zone” occurs on wider parts of the reef where sediment debris and algae form a definite pattern normal to the reef edge. A shallow “inner moat” occurs inside the rim, partly filled with clumps of living coral, boulders, and sediment. From here, the floor deepens gradually and tends to be covered with white coral sand of the “sanded zone.” Farther out in deeper waters of the lagoon, only a few larger coral heads reach the surface. This typical morphological sequence is also reported by Agassiz (1898).



The **barrier platform reefs** occur south of about 16° latitude, providing a distinct change in reef morphology from ribbons in the north to irregular-shaped patch or platform reefs. Fairbridge (1950) reports that they occur about 5 km or more from the 200-m isobath and seem to be separated by deep channels. Fairbridge does not elaborate on the morphological or ecological zones because he reports that they are less clear and not well known here.

### Atoll reefs

Fairbridge (1950) uses the term “atoll” in an exclusively morphological sense in reference to ring-shaped ribbon reefs that enclose a central lagoon. He reports that there is no marked difference in appearance between an “annular reef” rising from an oceanic cone or platform and one rising from the continental shelf. The most morphologically perfect atolls occur on the Northwest Shelf in the Indian Ocean and on the Sahul Shelf. Examples of the former include Mermaid, Clerke, and Imperieuse reefs. Scott Reef on the Sahul Shelf is a *paired atoll* containing one annular reef in the north and a horseshoe reef in the south. Seringapatam Reef, on the other hand, is a *perfectly enclosed reef* with a central lagoon that is approximately 36 m deep. Fairbridge (1950) reports that in section the reef is similar in morphology to the outer-barrier ribbon reefs of Queensland, except that it is about 300–1,200 m wide. Boulders occur along the reef crest and small shingle forms “hammerhead” spits. The wide reef flat accommodates the radial zone that is produced by algae, boulders, and sediment. A “sanded zone” breaks up into coral patches towards the lagoon.

Fairbridge classifies the Houtman Abrolhos group off northwestern Western Australia in the Indian Ocean (29° S.) as “shelf atolls” (Fairbridge, 1950, p. 342). The four groups from south to north and in decreasing order of size are the Pelsart, Easter, Wallaby, and Northern groups. These complex reefs, irregular and discontinuous, are essentially annular. Classification of these reefs is complicated by the fact that in the Pelsart group they have cores of eroded (truncated) Pleistocene reef material. Pleistocene coral limestone is also marginally exposed on the islands but is overlain by and replaced in the interior by a lagoonal limestone (a white calcareous mudstone). According to Fairbridge (1950), other groups in the Abrolhos differ morphologically from the Pelsart but appear to have gone through the same evolutionary sequence. In many cases, however, it is difficult to ascertain for classification purposes which parts of these reefs are contemporary and which are Pleistocene in age.

*Shelf atolls*, which occur on the Queensland Shelf near Cape Melville and on the Sahul and Rowley Shelves off northwestern Australia, may have volcanic foundations, be set on salt dome prominences, or simply have grown up from Pleistocene platform reefs (Fairbridge, 1967). On the surface, shelf atolls are morphologically similar to mid-Pacific atolls, but they definitely rise from the shelf instead of being founded at 1,200–1,500 m depths.

*Compound atolls* occur where continental crustal segments have slowly subsided, allowing barrier and platform reefs to grow upwards in the same manner as atolls. The Houtman Abrolhos Islands on the Western Australian shelf in the Indian Ocean contain parts of old coral reefs that are exposed, deeply weathered, and penetrated by deep holes (former karst pipes and solution holes).

*Oceanic Atolls* are the so-called mid-Pacific type, which rise from isolated volcanic cones in the deep ocean basins (e.g., from seamounts or guyots) with 1,200–1,500 m of accumulated reef growth. Fairbridge (1967) reports that these are quite rare in the Australian region but some are known in the Coral Sea and in the northern part of the Tasman Sea (Elizabeth, Middleton Atolls).

### Patch or platform reefs

The most numerous of the coral reefs around Australia and quite distinct from the fringing reefs, barrier types, and atolls, these reefs are without islands and are largely awash except at low tide. Fairbridge (1950, 1967) applied the term “patch reef” (also referred to as shelf, bank, table, or hummock reef) to the smaller ones (<2 km long) and “platform reef” to the larger ones (>2 km long). He emphasized that the adjective “platform” only means that the reef has a broad, flat, tabular morphology and that the term does not have any genetic significance because it does not imply growth from an antecedent platform. Most of these reefs occur in the GBR lagoon, in the Torres Straits almost blocking the channel between Australia and Papua New Guinea, and scattered along the northern edge of the Sahul Shelf. Deeper water reefs in about 30 m water depth on the interior of the Sahul Shelf off the rocky northwest Kimberly coast, such as the West Holothuria reefs and Long Reef, rise from submerged banks or terraces and are classified as platform reefs. Numerous others lie offshore from northwestern Australia in the Dampier Archipelago, and intermittently down the coast to the Northwest Cape where small patches occur in association with the Western Australian “sandstone reefs” and the Abrolhos atoll groups.

Because these reefs formed without islands, they lack features such as sand cays, shingle banks, and raised reef remnants, and their surface is simplified. From the reef crest, for example, just behind the breaker line, there is a broad, radially striated “trickle zone” of sediment debris and algae. Within the trickle zone there may be well-defined sand flats consisting of bare expanses of coral sand and small boulders that are interrupted by shallow pools fringed or carpeted by growing coral, *Mollusca*, *Halimeda*, and *Zostera*.

### Coral reefs with islands

Australian reefs contain islands comprised of calcareous fragmental coral, molluscan, algal, or foraminiferal sand or coral shingle. Classification of coral reefs with islands is somewhat complicated, as there were other attempts prior to Fairbridge’s effort. Steers (1929), for example,

classified islands with mainland bedrock as “continental” or “high” islands, whereas Hedley and Taylor (1908) referred to them as “hilly timbered islands”. Spender (1930) classified true coral islands into five types: islandless reefs with scattered debris only, (2) reefs with a sand cay but no shingle ramparts, (3) reefs with sand cay and ramparts but with no vegetation on the latter, (4) reefs with sand cay and ramparts with vegetation, and (5) reefs with all the features of class 4 together with a mangrove swamp on the reef flat. Steers (1937) later adopted Captain Cook’s term “low wooded island” for Spender’s Class 5, subdividing those with mainly sand and beach rock and those prevalently with shingle. With these classifications in mind and based on his own field experience, Fairbridge presented a revised classification of coral island types. Type 1 (Sand Cay, Unvegetated) refers to those islands that are commonly unstable and which migrate seasonally. They are found in all areas except on fringing reefs. Type 2 (Sand Cay, Vegetated) refers to islands that are moderately stabilized with beach rock. They are widely distributed but generally lacking in the outer reefs. Type 3 (Shingle Cay, with or without Vegetation) identifies moderately stabilized islands that are widely distributed but found mostly on smaller, more exposed reefs. Type 4 (Sand Cay with Shingle Ramparts) are unvegetated to vegetated islands, including mangrove swamp. Although restricted to smaller reef platforms in protected areas of the northern GBR lagoon, this category overlaps Type 5, as small pavements or promenades (benches) of older emerged reef-core material are commonly associated with the rampart system (Steers, 1937). Type 5 (Island with Exposed Platform of Older, Emerged Coral-Reef Material) takes in reef islands with or without a fringe of recent sand or shingle beach ridges or ramparts. The platform is vegetated and stable. In the 1967 book chapter (*Landform Studies from Australia and New Guinea* edited by J.N. Jennings and J.A. Mabbutt), Fairbridge more elegantly classifies reef islands into five categories: (1) Simple Sand Cays, (2) Vegetated Sand Cays, (3) Shingle Cays, (4) Sand Cays with Shingle Ramparts, and (5) Emerged Reef Islands.

## Conclusions

Coral reefs of the Australian shelf region are classified by Fairbridge into four principal types based on morphology: fringing, barrier, atoll, and platform. These terms have no genetic implication. Coral reef islands are classified in terms of five basic types: unvegetated sand cay; stable, vegetated sand cay; shingle cay; sand cay with shingle ridges or ramparts on the reef platform; coral islands with partly eroded core of older emergent coral limestone. Reef morphology is controlled by winds, waves, and currents. The stages of reef evolution range from initial patch reefs and crescentic or horseshoe patch reefs. Following these stages the larger (semi-atoll) and smaller (horseshoe-shaped reef) types develop differently, the former margining into a complete atoll which is followed by an infilled platform reef. The end stage of horseshoe-shaped

reefs is a small oval reef platform. Reef platform shape is also influenced by antecedent geomorphological and structural features. Coral islands on the Australian shelves form by accumulation of sand or coral shingle under wave action to form cays or by eustatic drop in sea level to expose older coral reefs. The Fairbridge (1950, 1967) classification of coral reefs on the Australian shelves supported, at that time, improved perspectives on the types of reefs and their geographic distributions in the eastern Indian Ocean, Coral Sea, Gulf of Papua, Torres Strait, Arafura Sea, and the Timor Sea. The Fairbridge classification for Australian coral reefs provided a stepping stone to further refinements and increased understanding of reef types, their spatial distribution patterns, and evolutionary modes.

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## Cross-references

[Antecedent Platforms](#)  
[Atoll Islands \(Motu\)](#)  
[Banks Island: Frasnian \(Late Devonian\) Reefs In Northwestern Arctic Canada](#)  
[Barrier Reef \(Ribbon Reef\)](#)  
[Beach Rock](#)  
[Boulder Zone/Ramparts](#)  
[Cay Formation](#)  
[Coral Reef, Definition](#)  
[Darwin, Charles \(1809–1882\)](#)  
[Fringing Reefs](#)  
[General Evolution of Carbonate Reefs](#)  
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[Great Barrier Reef Committee](#)  
[Lagoons](#)  
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[Mangroves](#)  
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[Vegetated Cays](#)  
[Western Australian Reefs](#)

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## REEF CLASSIFICATION BY HOPLEY (1982)

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### Definition

Classification is an analytical procedure denoting the typology of coral reefs based on factors such as morphology, age, size etc. The classification described here is derived from the evolution of continental shelf reefs on the Great Barrier Reef during the Holocene.

### Introduction

By the early 1980s, reef classifications derived from the morphologies of the Great Barrier Reef (GBR) reefs were available. Notably, these were

1. The relatively simple model of Fairbridge, which showed reefs developing from initial patches under the influence of prevailing winds and waves into larger platforms (see Entry *Reef Classification by Fairbridge (1950)*, this volume) and
2. That of Maxwell (1968), which had the advantage of aerial photography of a large proportion of the GBR. Again, small reef patches are extended by prevailing wind and waves but the larger platforms are not the end result, which, instead, is a complex form termed

as “resorbed” reef formed from the degeneration of a previous reefal mass.

Subsequent to these two classifications, there became available during the 1960s and 1970s much greater understanding of reefal processes and environments. In particular was the influence of the 1974 paper by Purdy which examined the karst features formed on reefs during long glacial periods of exposure and which showed the influence of these features during the Holocene transgression when rising sea levels recolonized the older Pleistocene foundations. A saucer shape with marginal rims around a central depression (the lagoon) was attributed to karst processes by Purdy and others. Isolated coral pinnacles evolved over tropical tower karst, spur, and groove as an expression of *lapiés* and blue holes as drowned dolines. The drowned karst theory played an important role in reef research during the 1970s and 1980s as the depth to the Pleistocene was determined by drilling and seismic investigation.

Also prominent at this time were new ideas on sea-level change, most prominently the influences of hydroisostatic shelf warping (e.g., Walcott, 1972; Chappell, 1974). The GBR was a particular focus of research, with various models of shelf warping published in the early 1980s (Chappell et al., 1982; Hopley, 1983). With modern sea level achieved about 6,500 years ago, higher sea levels (ca. 1 m) were found along much of the inner shelf due to hydroisostasy, while, where the shelf was wide, outer shelf submergence occurred (for review of latest mid-Holocene sea levels on the GBR, see Hopley et al., 2007).

Rates of reef growth from both dated drill cores (Davies, 1983; Davies and Hopley, 1983) and alkalinity anomaly measurements (Kinsey, 1985) also provided data which could be fed into evolutionary reef classification. By the late 1970s, aerial photography at a scale of about 1:60,000, was available for the whole reef, intended to aid in the management of the Great Barrier Reef Marine Park (GBRMP), set up in 1975. It was from this very large dataset and the greater understanding of reef development that the Hopley (1982) reef classification scheme developed. Subsequent to the formulation of the classification, a gazetteer was compiled for the Great Barrier Reef Marine Park Authority (GBRMPA), upon which analysis of the GBRMP was subsequently undertaken (Hopley et al., 1989). This was additional to the first comprehensive mapping of the GBR based on LANDSAT satellite imagery of the 1970s.

### Background to the evolutionary classification

The basic presumption of the 1982 Hopley reef classification is that during the final phases of the Holocene transgression, Pleistocene reefal foundations that had been subaerially exposed for much of the time since the last interglacial were slowly drowned and recolonized by a Holocene veneer. Modal accretion rates were about 7–8 m/1,000 years (Davies and Hopley, 1983), so that where reefs commenced growing from relatively shallow



(<12 m) foundations, a “keep up” mode of growth was possible (see Macintyre and Neumann, this volume). Once reefs reached sea level, vertical growth was converted to lateral growth and sediment movement. Thus, reefs growing from shallower karstified surfaces tend to be more mature in the evolutionary sequence than ones growing from deeper foundations.

This classification is set within the sea-level mode of the GBR, i.e., modern sea level first achieved about 6,500 years ago, possibly a little higher on the inner shelf and a little lower on the outer shelf. The result is for inner shelf reefs to be more mature with low wooded islands which retain evidence of higher sea levels in the form of micro atolls and cemented platforms. On the GBR, the area of youngest reefs is where the Pleistocene foundations are deepest (<20 m) and hydroisostatic subsidence is active (Chappell et al., 1982; Hopley, 1983; Lambeck and Nakada, 1990).

Although the classification published in 1982 was derived from the data and environment of the GBR, it has been tested on other reefs and is applicable to most continental shelf reef systems taking into account Holocene sea-level history, depth to the Pleistocene foundations, and the size of reefs involved as discussed below.

### The 1982 evolutionary reef classification system (Figures 1 and 2) (Hopley, 1982; Hopley et al., 2007)

Evolving from the recolonization of Pleistocene foundations, the classification identifies three phases:

1. *Juvenile* – mainly upward growth and enhancement of the Pleistocene relief
  - (a) Unmodified antecedent platforms
  - (b) Submerged reefs – reefs with some Holocene growth, mainly on the highest parts of the antecedent platform but not reaching modern sea level
  - (c) Irregular reef patches – patchy reef flat development from the highs in the antecedent platform
2. *Mature* – horizontal extension of the modern reef flat
  - (d) Crescentic reefs – coalescence of patch reefs on the most productive windward margins to produce a crescentic shaped reef with open back reef area
  - (e) Lagoonal reefs – extension of the reef flat around the most productive margins of the foundations to enclose or partly enclose one or more lagoons
3. *Senile* – masking of the original Pleistocene relief
  - (f) Planar reefs – infilling of lagoons by internal patch reef growth and sediment transported from windward margins to produce extensive reef flat, eventually with a widespread sediment blanket. Islands can form at this or earlier stages with appropriate area of reef flat and wave transport.

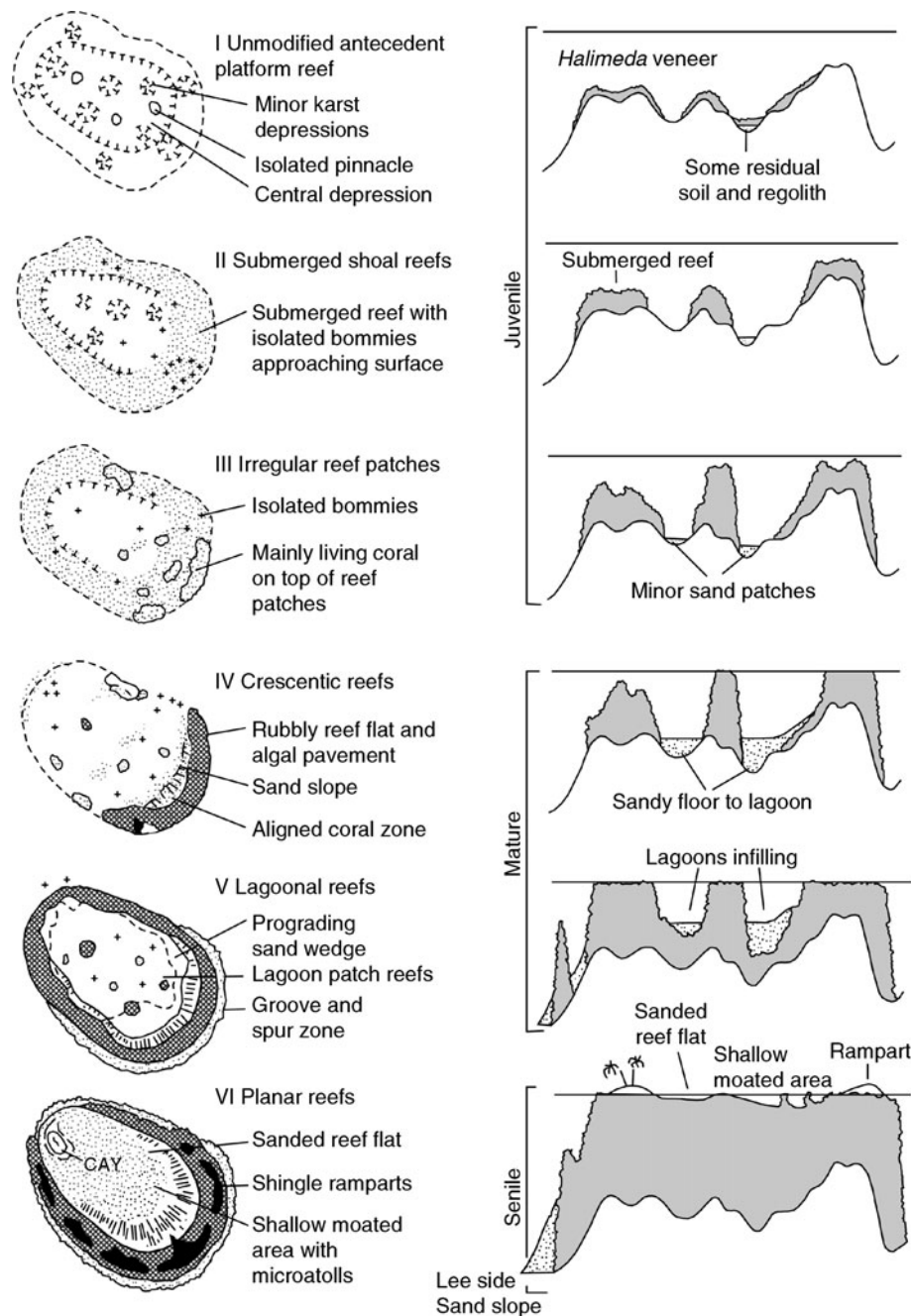
Not all shelf reefs will be included in this classification, the main focus of which was to identify a sequential model of reef development and eventually the rate at which reefs

progress through the system. Other reefs that need a separate classification include fringing reefs (Smithers et al., 2006) and linear barrier or ribbon reefs which, apart from their relationship with sea level, are difficult to place in an evolutionary sequence. However, within the GBR Marine Park, there are 2,877 shelf reefs (Hopley et al., 1989) excluding fringing and ribbon reefs, providing an unmatched dataset for the development of an evolutionary model of reef classification (numbers from the new GBRMPA GIS dataset analyzed in Hopley et al., 2007). For many of these reefs, there is information from drilling, dating, and seismic profiling which, together with estimates of calcification rates, allow calculation of the rate of reef growth and progression, from one morphology to the next in the sequence (see Hopley et al., 2007, Chapter 8).

### Rates of reef growth and evolutionary change

The rates of reef morphological change (Hopley et al., 2007, Chapter 8) are influenced by a number of factors:

1. The depth of the Pleistocene surface is up to 30 m below present reef flat level, the deeper foundations being drowned earlier by a rapidly rising sea level and adopting a “catch up” mode (see Macintyre and Neumann, this volume) while shallower foundations were drowned by a more slowly rising sea level and adopted a “keep up” mode. Radiocarbon dates from the upper 3 m beneath the reef flat have a very strong correlation with depth to the antecedent surface, with shallow foundations producing reef top ages of 6.5–5.5 ka and deeper foundations progressively younger. On small reefs (<1.5 km<sup>2</sup>), reef flats evolved rapidly as reef top patches coalesced into crescentic reefs on windward margins.
2. In reefs where drilling and dating data are sufficient to draft isochrons, smaller reefs (<1.5 km<sup>2</sup>) may evolve directly from reef patches to planar reefs as the patches coalesce over the whole reef platform. On slightly larger platforms, the transformation from patch to crescentic is about 700 years and from crescentic to lagoonal ca. 1,350–1,800 years (Hopley et al., 2007).
3. Progression from lagoonal to planar reef is a more complex process, as lagoonal infilling comes from both internal growth of patch reefs (the most rapid framework construction within the reef, Davies and Hopley, 1983) and sediments derived from the reef rim. There are three sedimentation modes:
  - (a) For the densely covered reef slope 10 kg m<sup>2</sup>/year, which converts to an upward accretion rate of 7 m/ka;
  - (b) For the reef flat, which converts to 3 m/ka, 4 kg m<sup>2</sup>/year. The reef flat, however, has a self-limiting width of 400 m (see Kinsey and Davies, 1979), which means that the area of productive reef flat to lagoonal area is much smaller on larger reefs, which hence have a slower infilling rate.

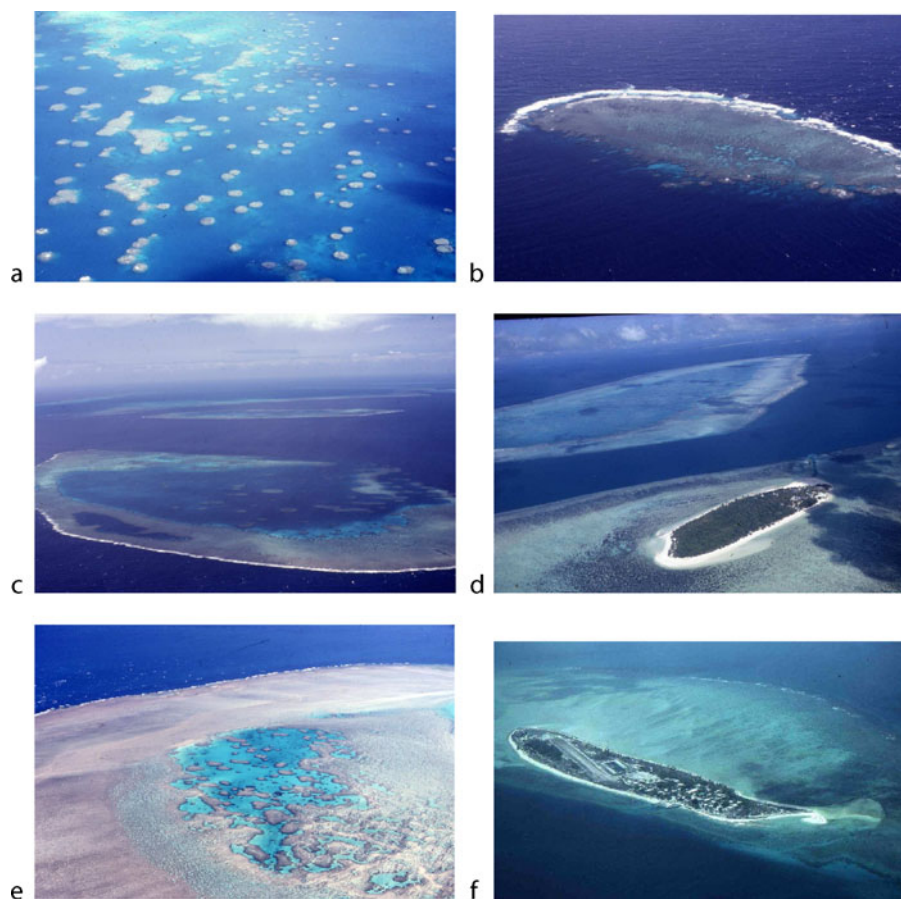


Reef Classification by Hopley (1982), Figure 1 Evolutionary classification of shelf reefs (Hopley, 1982).

- (c) Productivity of the lagoon is low at  $<2 \text{ kg m}^{-2}/\text{year}$  producing only a  $1.5 \text{ m/ka}$  infilling rate (Kinsey, 1985).

The dataset used by Hopley et al. (2007) included reefs with areas of  $1.9\text{--}18.1 \text{ km}^2$  with representative diameter values of  $1\text{--}5 \text{ km}$ , thus illustrating the much smaller area of reef flat: lagoon for larger reefs. Larger reefs have younger reef top ages, providing a strong negative correlation.

Smallest reefs in the GBR with shallow foundations have progressed from lagoonal to planar stages in  $1,000\text{--}2,000$  years. For larger reefs with deeper foundations, the time required has been  $>5,000$  years. For reefs with more than  $20 \text{ km}$  diameter and with a Pleistocene foundation  $20 \text{ m}$  deep, the suggested time required is  $>10,000$  years. Such reefs may have inherited their morphology from a previous interglacial, and with interglacial



**Reef Classification by Hopley (1982), Figure 2** (a) Reef patches – GBR off Innisfail. (b) Crescentic reef – Viper Reef, GBR. (c) Open lagoonal reef – GBR off Bowen. (d) Infilling closed lagoonal reefs – Heron and Wistari Reefs, GBR. (e) Remnant lagoon – Redbill Reef, GBR. (f) Planar reef – Coconut Island (Poruma), Torres Strait.

periods being about 10,000 years long, there may have been insufficient time for major changes in morphology within the Holocene or any other recent interglacials.

## Conclusions

The analysis of changing morphology of Holocene reefs of the GBR appears to justify the presented evolutionary model of reef classification. Purdy and Gischler (2005) suggested that uplift could accelerate the lagoonal infilling stage and this would appear to be confirmed by the GBR. Planar reefs representing the end stage of the classification are clearly more numerous on the inner shelf (see Hopley et al., 1989) where hydroisostatic uplift has been demonstrated (e.g., Lambeck and Nakada, 1990). However, all stages in the classification exist, indicating the range of controlling conditions on the GBR – reef size, depth to the antecedent surface, and rates of calcification processes. Small variations may occur, for example, through contrasting Holocene sea-level histories, but the influences described are global and the classification is applicable to most shelf-reef systems.

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## Cross-references

[Antecedent Platforms](#)  
[Carbonate Budgets and Reef Framework Accumulation](#)  
[Coral Cay Classification and Evolution](#)  
[Density and Porosity: Influence on Reef Accretion Rates](#)  
[Glacio-Hydro Isostasy](#)  
[Holocene Reefs: Thickness and Characteristics](#)  
[Reef Classification by Fairbridge \(1950\)](#)  
[Reef Classification by Maxwell \(1968\)](#)  
[Solution Unconformities](#)

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## REEF CLASSIFICATION BY MAXWELL (1968)

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### Definition and Introduction

Classification proposed by Darwin (1842) recognizes three classes, namely, fringing, barrier, or atoll ignores the multitude and diversity of those continental shelf reefs, which fall between the fringing reefs and the outer barrier reefs near the shelf edge.

Fairbridge (1950, 1967) attempted a genetic classification of these shelf reefs, which would normally fall within the barrier reef type of Darwin (Hopley, 1982).

Maxwell (1968) attempted to elaborate further on the Fairbridge classification scheme, and both believed that they could observe gradational patterns “that lend support to the view that they represent various stages in reef development” (Maxwell, 1968). As Hopley (1982) points out, the classifications were “based on organic and sedimentary growth in response to prevailing wind and wave

conditions during a single period of relatively stable eustatic sea level,” and the reefs had developed exclusively during the Holocene. There was appreciation of the subsequently recognized importance of substrate control of the shape of underlying older reef morphology including antecedent platform shape (Hoffmeister and Ladd, 1944) or karst (Purdy, 1974).

Maxwell (1968, p. 101, Figure 65) recognized the following shelf reef types:

Circular – elliptical shape, radial growth  
 Platform  
 Elongate platform  
 Lagoonal platform  
 Elongate shape  
 Wall  
 Cusplate  
 Prong  
 Composite apron  
 Open ring  
 Open mesh  
 Closed ring  
 Closed mesh  
 Resorbed shape  
 Resorbed

In addition, Maxwell (1968) recognized the high reef of the inner shelf which elsewhere is thought of as being an island namely a “low wooded island.”

The classification scheme envisaged that reefs develop downwind detrital wedges of sediment when in plan resemble horns, which on larger reefs will coalesce to enclose lagoons, and which over time will become infilled with reef sediment to produce platform reefs. Eustatic sea-level variations play little or no part in the morphological variations. Maxwell (1968, p. 100, Figure 64) inferred that the ultimate fate of the reef was “resorption” or chemical dissolution and erosion or reef decay.

### Summary

A considerable amount of research on reef morphology and reef substrates was undertaken in the early 1970s (Flood, 1977; Flood and Orme, 1977), and today it is accepted that the Maxwell (1968) classification is not an evolutionary scheme of morphological development. A more realistic classification of the shelf reef has been presented by Hopley (1982, p. 253, Figure 9.2).

It is now realized that the resorbed shape of Maxwell is indeed the initial stage of Holocene reef growth situated on a pre-Holocene reefal platform where coral colonization during the Holocene sea-level rise has not formed a complete perimeter barrier to the action of waves and that some of the isolated coral growth has occurred on pinnacles of karst towers on the underlying preexisting Pleistocene reef.

An additional modification of the coral reef surface on the circular-elliptical shaped reefs is the “low wooded islands” type of morphological modification, which is characterized by the extensive presence of mangroves. This is a very late stage of modification to the reef-top surface,

and it appears to be related to mangrove colonization subsequent to a slight fall in sea level. These “*low wooded islands*” are common on the inner shelf of the northern Great Barrier Reef, on the reefs within Moreton Bay near Brisbane, and throughout the coral reefs of Southeast Asia and in some inner shelf reef of Belize. Hopley (1982, p. 250, Figure 9.1) of Flood and Orme (1977) depicted in a schematic way, the currently perceived morphological evolution of shelf reefs as a function of tectonic, isostatic, Eustatic, and biological growth factors.

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## Cross-references

[Antecedent Platforms](#)  
[Darwin, Charles \(1809–1882\)](#)  
[Global Ocean Circulation and Coral Reefs](#)  
[Reef Classification, Response to Sea Level Rise](#)  
[Last Glacial Lowstand and Shelf Exposure](#)  
[Low Wooded Islands](#)  
[West Indian Coral Reef Classification](#)

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## REEF CLASSIFICATION, RESPONSE TO SEA LEVEL RISE

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## Definition

This is a classification of coral reefs based on their response to rising sea levels.

## Introduction

Coral reefs can be classified according to their ability to cope with the post-Pleistocene rise in sea level. Their response to rising sea level is governed by many factors: notably, composition of reef-building communities, changes in the rates of sea-level rise, topography of the substrate when reef growth is initiated, and stress from inimical waters in reef lagoons (Neumann and Macintyre, 1985). The response patterns of reefs have been well documented in studies of reef-growth histories in the Atlantic/Caribbean region but apply to other ocean areas as well. These patterns can be described by a simple analogy comparing reefs to a group of joggers in a race against sea level (Neumann and Macintyre, 1985). Those able to keep pace with the rising sea level are “Keep-Up” reefs; those coming up from behind are “Catch-Up” reefs; and those that are unable to keep up and are left behind exhausted are “Give-Up” reefs (Figure 1).

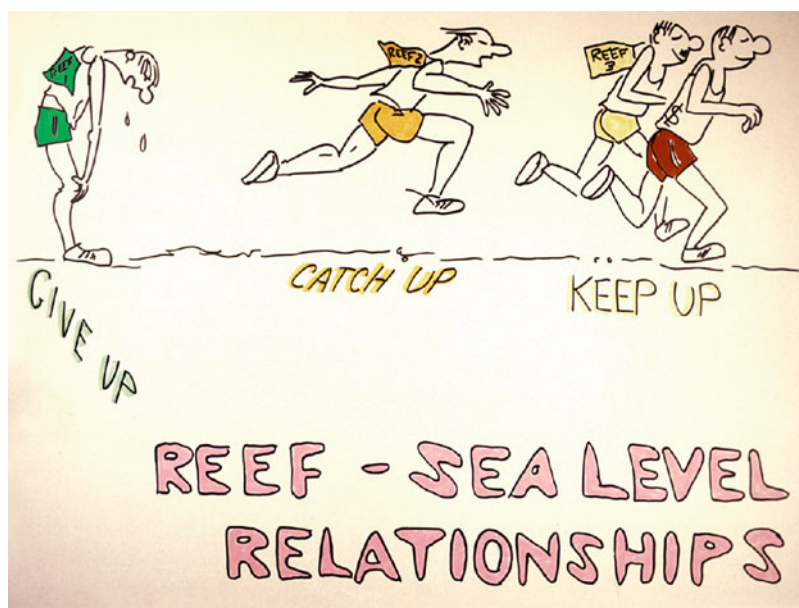
## The classification

**Keep-Up Reefs.** These reefs have maintained their crests in shallow water throughout their history of accumulation. They usually occur near the shore and were formed during the late phase of the post-Pleistocene sea-level transgression, when there was a significant decrease in the rate of sea-level rise. In the western Atlantic, these reefs are dominated by *Acropora palmata*, a species that is able to accumulate fairly rapidly in exposed areas under heavy wave action. One of the best examples of a “Keep-Up” reef is the fringing reef off Galeta Point, Panama (Macintyre and Glynn, 1976).

**Catch-Up Reefs.** This type of reef establishes itself in deeper water and subsequently catches up with the sea surface because the reef facies accumulates faster than the rise in the sea level. In the western Atlantic, such reefs are usually dominated by the branching coral *Acropora cervicornis*, which can flourish in depths up to 15 m. These reef types are subject to damage and transport by storm activity and thus occur mainly in protected settings, such as Alacran reef of Yucatan (Macintyre et al., 1977) and the Belize Barrier Reef lagoon (Macintyre et al., 2000).

**Give-Up Reefs.** These are usually deeper-water reefs whose growth has been interrupted, thus leaving them stranded in water, too deep for reef accumulation to occur. Stress factors are usually responsible for terminating reef growth, particularly turbidity and low temperatures caused by the flooding of platforms leeward of the reefs. Deeper outer-slope reefs were left stranded by rapid sea-level rises associated with “fresh-water pulses” (Fairbanks, 1989). These deep-water relict reefs are well documented on the insular shelves of the eastern Caribbean (Macintyre, 1972).

A similar classification was proposed by Davies and Montaggioni (1985) for Pacific reefs, particularly those from the Great Barrier Reef.



Reef Classification, Response To Sea Level Rise, Figure 1

### Summary

Coral reefs can be classified by their response to the postglacial rise in sea level, which governs the path of their development and composition of present-day surface communities.

[Reef Classification by Maxwell \(1968\)](#)  
[Sea Level Change and Its Effect on Reef Growth](#)  
[Sea-level Indicators](#)  
[West Indian Coral Reef Classification](#)

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### Cross-references

[Darwin, Charles \(1809–1882\)](#)  
[Reef Classification by Fairbridge \(1950\)](#)  
[Reef Classification by Hopley \(1982\)](#)

### REEF DRILLING

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### Synonyms

Boring; Coring; Reef coring

### Definition

Reef drilling is a method that recovers samples from the interior of a reef, typically using a rotary apparatus operated on the sea floor by divers or from a surface vessel.

### Background

Dating to the writings of DaVinci in the fifteenth century and Mojsisovics' description of alpine reefs four centuries later, natural philosophers asked two fundamental questions: (1) how do we explain oceanic deposits found so far above present sea level, and (2) how did organisms that were limited to the upper few hundred meters of the ocean create deposits that are hundreds or even thousands of meters thick? Tectonic uplift provided a widely accepted answer to the first question. In contrast, the role of subsidence in creating thick reef deposits triggered a heated debate among nineteenth and early twentieth century reef scientists such as Darwin (1842), Geike (1883),



Guppy (1888), Murray (1889), Agassiz, (1902), Gardiner (1904), Daly (1915), and Davis (1923). The main obstacle for Darwin's subsidence theory was the fact that any evidence logically existed beneath the sea and could not be directly observed. The deductive methods championed by Lyell (1830) were not yet accepted by either the body of strict empiricists (e.g., Alexander Agassiz) or those still seeking explanations in one or more "great floods" (e.g., Alexander's father, Louis). The answers were to remain in the submerged strata and beyond the limits of direct observation for a century after Darwin's first suggestion of subsidence as the dominant factor in atoll formation.

While traditional drilling has been in use since at least the nineteenth century, coring to chronicle the interior of modern or Quaternary reefs is relatively new. The Funafuti borings, commissioned by the Royal Society and described in a 1904 issue of *Nature*, were designed more to address Darwin's subsidence hypothesis than to elucidate the relationship between modern reef environments and their ancient counterparts. Half a century later, the shallow-marine carbonates that dominated the upper intervals of the US Geological Survey cores through the Marshall Islands (Ladd and Schlanger, 1960) were simply cataloged as "reefal limestones" and placed in storage once the all-important basalt foundation was encountered, vindicating Darwin's controversial ideas.

So entrenched was the focus on the relative roles of sea-level change (Daly, 1915) versus tectonics (Darwin, 1842) that, as late as 1928, the preeminent geographer William Morris Davis still characterized his chance to observe the surface of the Great Barrier Reef through a viewing box as "an entertaining experience but, as might have been expected, entirely fruitless as far as the origin of the reef is concerned" (described in Hopley, 1982). Two events would change this view forever. The first, the introduction of Emil Gagnan's demand regulator in 1943 (Lawrence, 1997), facilitated direct submarine observations and foreshadowed the rapid rise of marine ecology. The second was the development of a small, submersible reef-drilling system by Ian Macintyre in the 1970s. For the first time, cost-effective and reliable access to the interior of modern reefs was now available.

The early studies of Ian Macintyre, Walter Adey, and Peter Glynn provided important foundations upon which all subsequent Holocene reef studies have built. Since the early descriptions of Holocene reef building in Panama (Macintyre and Glynn, 1976), cores have been recovered from throughout the Caribbean (Adey and Burke, 1976, 1977; Macintyre 1988; Macintyre et al., 1985; Hubbard et al., 1997), Florida (Shinn, 1980; Shinn et al., 1989), French Polynesia (Montaggioni et al., 1997; Cabioch et al., 1999), Hawaii (Grossman and Fletcher, 2004), the western Pacific (Cabioch, 2003), the Great Barrier Reef (Davies et al., 1985; Hopley et al., 2007), the Indian Ocean (Camoin et al., 1997; Montaggioni and Faure, 1997; Braithwaite et al., 2000), and Japan (Yamano et al., 2001), among others.

Early coring studies emphasized the large-scale evolution of facies patterns and reef fabrics that might be integrated into hydrocarbon exploration models. This focus quickly broadened to include the role of ocean processes and changes in sea level in controlling reef development on a millennial scale. More recently, attention has shifted to the dramatic decline in the world's reefs, with fundamental questions being asked about the mechanisms that are responsible and the extent to which anthropogenic factors have been in play. In the words of Wendell Berry, "We cannot know what we are doing until we know what nature would be doing if we were doing nothing" (*Home Economics*). Cores through Holocene reefs provide our only possibility to examine reefs that were identical to those of today, except for a notable lack of human influence. Thus, they provide opportunities to make links with the past, to understand the origins of present-day reefs, and to make projections about how increasing anthropogenic pressures may change reef trajectories in the future.

The following focuses on three topics. First, the drilling method is generally described. The intent is not to provide a "how to" primer, but to describe the methodology in its most basic form. Second, an overview of the ways that reef cores can be used describes the kinds of information that can be derived from them. And finally, potential issues with extrapolating from cores to the larger reef interior are considered. It is important to understand problems that are inherent in this approach. Nevertheless, we need to be mindful that reef cores pretty much represent "the only game in town" when it comes to examining the underpinnings of the present-day coral-reef community or the events that have led up to where we find ourselves today.

Early bore holes along the northern Great Barrier Reef (Richard and Hill, 1942; Maxwell, 1962) provided information on the evolution of that carbonate system. Since then, large shipboard systems have made significant contributions to our understanding of the larger-scale questions that dominated the nineteenth and twentieth centuries. Longer-term platform evolution along the Great Barrier Reef was detailed using deeper cores through the outer Great Barrier Reef (Webster and Davies, 2003; Braithwaite et al., 2004). Cores through the deep reefs off Barbados have provided invaluable information on patterns of sea-level change that extend beyond the histories derived from reefs within the range of normal Self Contained Underwater Breathing Apparatus (SCUBA) diving. This chapter focuses on the more modest systems that have provided so many of us with an opportunity to carefully examine the relationships between reef fabric, oceanographic process, and rising sea level over the past 12,000 years.

### The coring method

While individual drill rigs vary in size, complexity and their ability to penetrate further into the reef, all owe their origins to the prototype developed at the Smithsonian Institution and described in Macintyre (1975). In this first

iteration, hydraulic fluid was delivered to a modified Ackley impact wrench via hydraulic hoses from a pump that was driven by a four-cylinder Triumph gasoline engine. Core was collected in a rotating barrel that was connected to the wrench. A separate pump provided water to the rotating drill bit for cooling and clearing away of debris generated by the drilling process. Over the years, researchers have experimented with different power supplies, larger ones for greater penetration, smaller ones for increased portability, but they all share the basic design of the original Macintyre system.

Core is typically recovered in 1.5-m (5-ft) sections, the most common length for commercially available core barrels (Figure 1a). Larger-diameter, single-walled barrels have been used to recover short reef cores or to sample individual coral heads. However, most reef-coring systems use a 10–15 cm (diameter), double-walled barrel in which an inner cylinder is isolated from its outer counterpart by a swivel that allows the core to slip into the stationary inner tube while the outer barrel and drill bit rotate to auger into the reef (Figure 2).

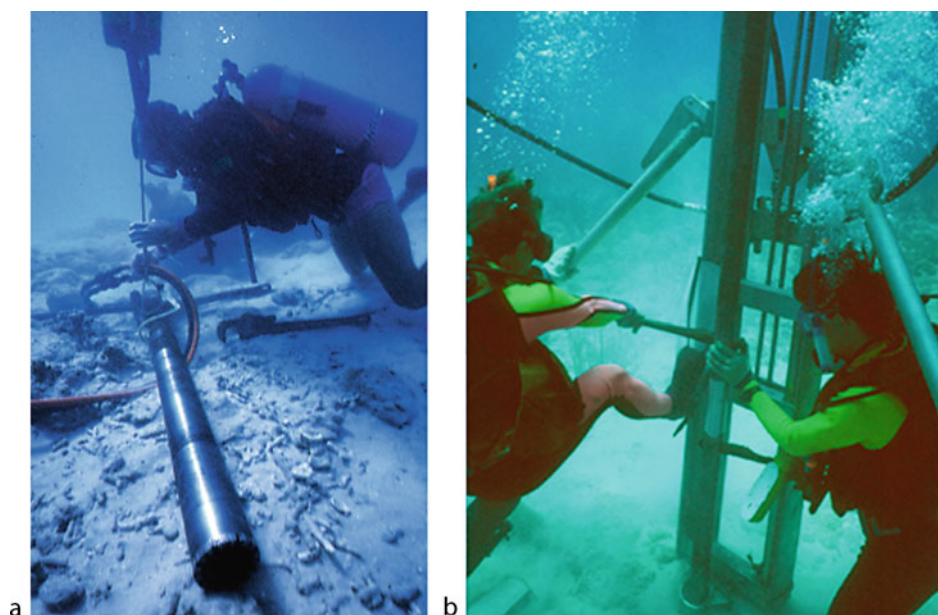
In earlier systems, smaller-diameter extension rods were added to the top of the core barrel after each recovery. In this method, the complete length of drill string had to be removed, section by section, each time a core was recovered. More recently, “wire-line” systems have been developed that allow remote recovery of the inner core barrel without removing the drill string. In these systems, the extension rods are of the same diameter as the core barrel. The uppermost section of drill pipe is

separated from the drill motor using pipe wrenches (Figure 1b), and a “messenger” is lowered through the interior of the drill string to lock onto and pull up the inner core barrel.

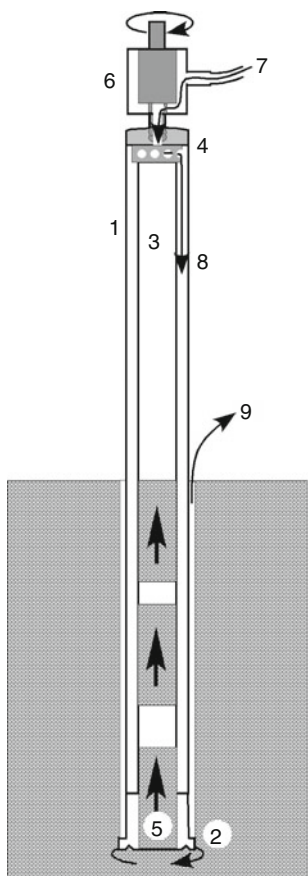
The advantage of this approach is threefold. First, it greatly reduces the time and effort required to recover the core. Second, because the extension rods stay in place throughout coring, they prevent contamination by material falling from the walls of the hole during core recovery. Finally, because the extension rods are of the same diameter as the outer core barrel, this eliminates the potential for cave-in to jam the core barrel at the point where the drill string changes size.

Once the core is recovered, each piece is numbered from top to bottom and marked to indicate its original orientation. Loose rubble is placed in bags that are likewise numbered in sequence. Notes describing changes in drilling difficulty throughout the core interval are used to create a log in which samples are placed into the best possible vertical context (Figure 3). Coral types are added, based on either field or laboratory determinations, and are ideally identified to species. To the extent possible, intervals of sediment, rubble, and open voids are placed on the log using the notes taken by the operators while drilling.

The earliest drilling systems were used primarily in shallow water and were suspended from a tripod (Figure 4), a configuration still used by many researchers. The drill and the core barrel are suspended on a wire, and a small hand winch is used to raise the drill after a core is



**Reef Drilling, Figure 1** (a) Typical core barrel for drilling. The bit in the foreground drills a hole in the reef. A sleeve inside the barrel is suspended on a swiveling mechanism that allows the core to slide into the stationary inner barrel (Fig. 2). (b) Divers breaking the joint between the core barrel and the first section of extension rod. This provides access to the inner core barrel using a “messenger” that is lowered into the hole (Photos by permission of the author).



**Reef Drilling, Figure 2** Diagram illustrating a double-walled core barrel drilling into the reef (stippled pattern). The outer assembly consists of a core barrel (1) and either a diamond or carbide drill bit (2). An inner barrel (3) is suspended on a swivel mechanism (4) that allows the inner sleeve to remain stationary while the outer cylinder rotates. As the bit grinds into the reef, samples (5) slide into the stationary inner barrel. A water swivel (6), attached to the top of the core barrel or the uppermost section of extension pipe allows water to enter from a stationary hose (7) while the inner mechanism maintains a connection between the drill string and the drill motor (not shown, but attached to the top of the water swivel). Water flow passes through channels in the swivel mechanism, moves down along the annulus between the inner and outer core barrels (8) and out along the edge of the drill bit. Small bits of debris generated by drilling plus any sediment are flushed out of the hole (9).

completed. The wire is usually left slack during drilling, and weight is added (often in the form of graduate students standing atop the drill motor: [Figure 4a](#)) to speed penetration. On exposed reef flats, unmodified commercial core rigs can be used ([Figure 5a](#)). In some cases, small platforms that can be raised on legs have been used to provide a dry environment for coring operations along the reef crest ([Figure 5c](#)). This requires additional logistical support and can be used only where water depth over the reef crest allows the platform to be floated into place. In deeper water, the simpler tripod can still be used or can be

replaced by an air bag that provides buoyancy to raise the drill string and move equipment on the bottom ([Figure 5b](#)). The lift bag can be combined with a block-and-tackle system that is attached to the substrate to apply constant pressure to the bit, a particularly difficult venture when coring horizontally as in [Figure 5d](#).

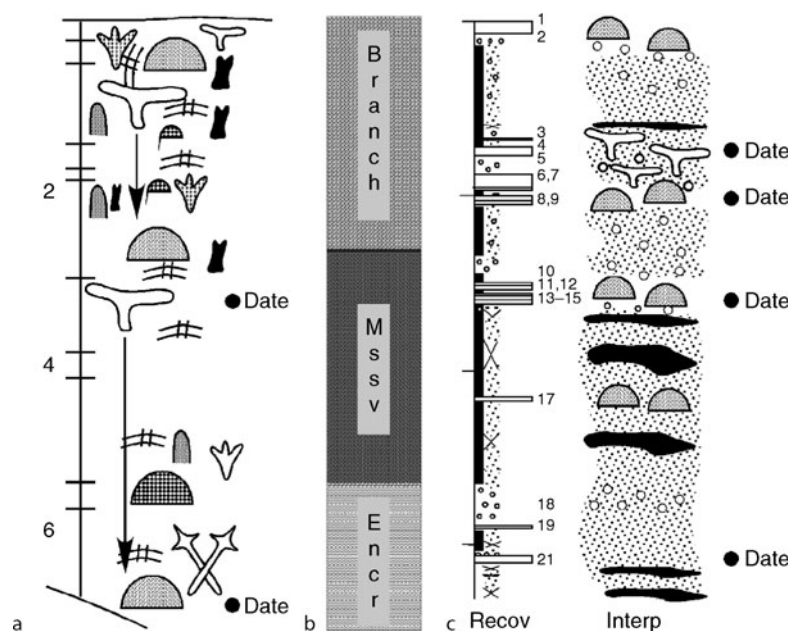
## What we have learned from reef cores

### Paleoenvironment

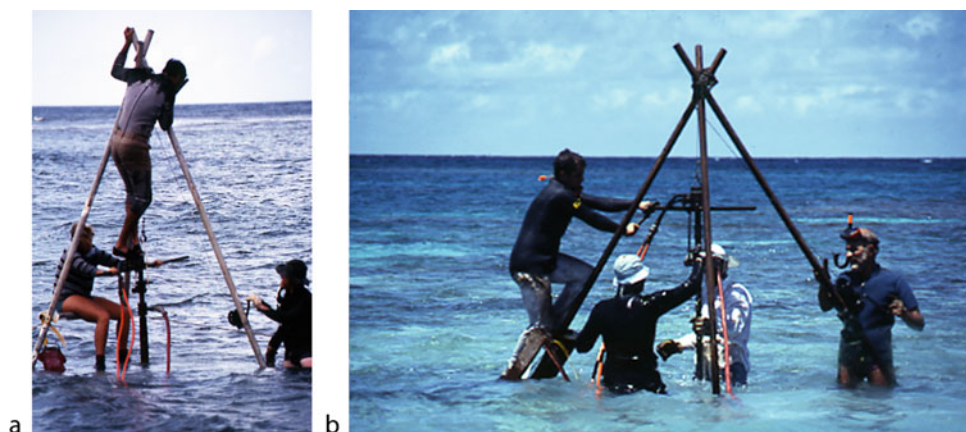
Coring is the primary method for directly sampling the interior of a modern reef. At the most basic level, a core tells a story of reef development at a single point. By taking multiple cores, the investigator can start to assemble a three-dimensional story. The present-day distribution of coral species (or morphologies) can be used to interpret which areas on a modern reef surface are represented by the corals recovered from its interior. Variations in coral type within a core may reflect changing water depth, shifts in wave energy or gradients in other physical- and chemical-oceanographic factors. Radiometric dating of individual coral samples provides a temporal context within which these changes likely occurred. Ideally, cores are taken along transects ([Figure 6](#)) to provide important information about spatial variability within the reef, as well as changes in reef morphology and community structure over time. Interpretations from a single core can provide an incomplete picture that is at odds with the larger fabric of the entire reef.

In the example provided in [Figure 6](#), from southwestern Puerto Rico, coral type is represented by open symbols (branching corals) and black semicircles (massive species). The dashed timelines, based on calibrated radiocarbon dates, represent the reef surface at 1,000-year intervals. At this site, the early reefs occurred close to the shelf edge and atop a shallower and broader platform some 30 m landward. They were populated by branching *Acropora palmata*, the dominant Caribbean reef crest species for the past million years. The lowest section of the reef is made up of debris derived from bioerosion of unpreserved corals that likely grew along the antecedent Pleistocene margin (the “brick” pattern). Based on available sea-level curves, the area had flooded by 12,000 years ago but, while corals were undoubtedly present, conditions after shelf flooding prevented reef accretion until sometime around 10,000 years ago. As the outer reef continued to build, massive corals formed in what was probably a protected backreef area behind the outermost ridge. *A. palmata* was the primary framebuilder at that time and remained so until circa 6,500 years ago, when reef accretion stopped along this and many other Caribbean shelf margins. The dominance of branching corals throughout the history of this reef is in marked contrast to the present-day reef community of mostly massive scleractineans and soft corals. More detailed information on the evolution of specific reefs and the paleoclimate associated with their development is provided elsewhere in this volume.





**Reef Drilling, Figure 3** Core logs from three different studies used to characterize the nature of the reef interior. (a) Generalized log showing the core intervals (horizontal ticks) and the dominant constituents found in each section of the core. Individual samples are not indicated. (b) Summary log delineating the interpreted facies (in this case, branching, massive, and encrusted corals). (c) Detailed log showing the specific locations and extent of each recovered sample (*left*), plus an interpretation of the cored section (*right*) based on recovered samples and detailed drilling notes.

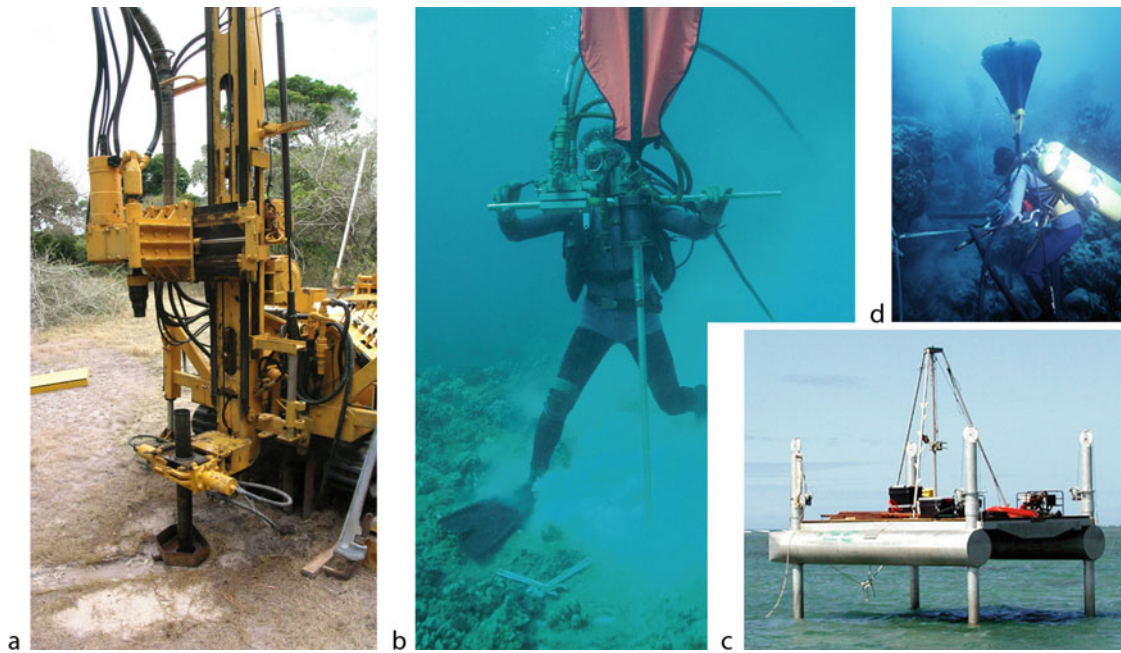


**Reef Drilling, Figure 4** Typical deployments of tripod-based drills on the reef crest (*left* – St. Croix, US Virgin Islands; *right* – Antigua). A hand-winch system is used to raise the drill string. The lifting wire is generally left slack and weight is added to facilitate drilling. Note the hoses that deliver water and hydraulic power from a system on a small vessel located nearby. This system has been operated from a 15-ft Boston Whaler at low cost and with minimal logistical support (Photos by permission of the author).

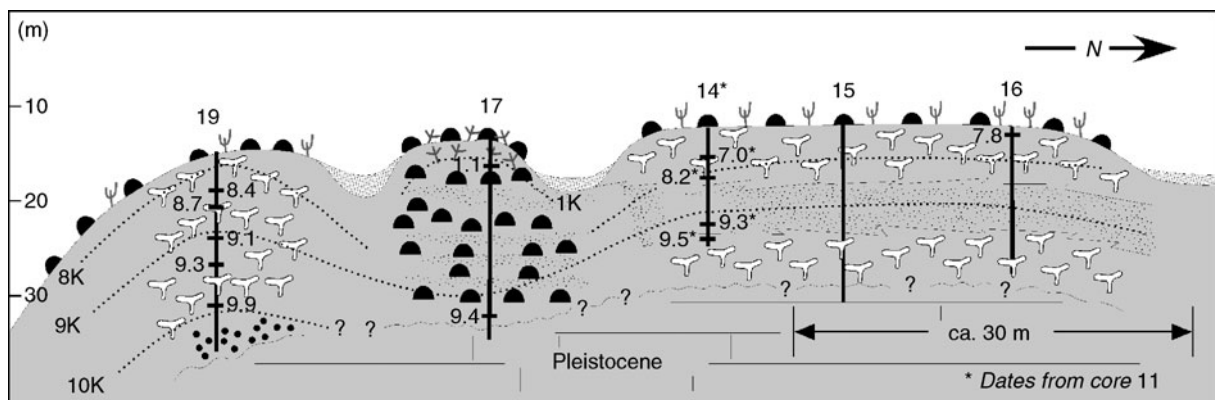
### Modern reef environments and fossil reef facies

When trying to understand a fossil reef, whether in outcrop or a series of cores, geologists think in terms of reef *facies* – visually distinct assemblages of preserved corals and sediment that can be related to the zonation patterns biologists see on the surface of the reef today. A reef facies is the rock equivalent of the environment of deposition in

which the preserved organisms originally lived and died. As will be discussed below, a number of factors conspire to make the end product in the geologic record an imperfect representation of what actually lived in and on the reef in the past. Nevertheless, if we confine ourselves to the primary constituents and keep some of these pitfalls in mind, we can make realistic inferences within an



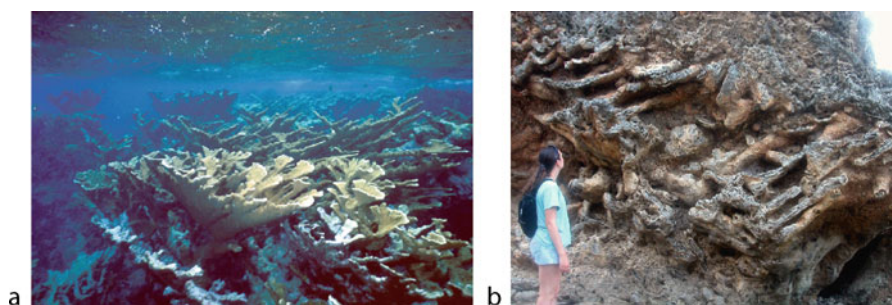
**Reef Drilling, Figure 5** Different coring systems in use today. (a) Land-based system used by French researchers to drill through Pacific and Indian Ocean atolls (Photo courtesy of Guy Cabioch). (b) In deeper water, the tripod can be replaced by an air bag that provides buoyancy to move equipment and lift the drill after coring is completed. (c) Along submerged reef crests, a small jack-up platform allows dry operation (Photos B and C courtesy of Charles Fletcher). (d) Drilling on the vertical wall of a submarine canyon required a lift bag and a block-and-tackle system. Cables run from the drill motor, through pulleys attached to the reef, back to a pulley on the drill motor, and then up to an inflated air bag. This action converts lift provided by the air bag into the inward force required to drill. This method has also been used in vertical deployments where simply adding weight to the drill is inconvenient (Photo by permission of the author).



**Reef Drilling, Figure 6** Cross section through a shelf-edge reef off the southwestern corner of Puerto Rico. The distribution of branching (white symbols) and massive corals (black hemispheres) reflects conditions that are favorable to each (e.g., distance from the reef front and paleo-water depth). Time lines (*dashed*) are based on corrected radiocarbon dates, and provide important information on surface morphology through time (From Hubbard (2008), with permission by Springer).

individual fossil reef or between reefs in different settings. For example, a preponderance of branching acroporids in a Quaternary Caribbean reef likely reflects moderate to high wave energy and low sedimentation in shallow water where light is abundant (Figure 7). Moving down the reef

front, a progressive shift toward species and morphologies that are better adapted to declining light, reduced wave action, and perhaps greater sedimentation creates a predictable pattern that can be used to relate facies within a fossil reef to environmental zones on the surface of the



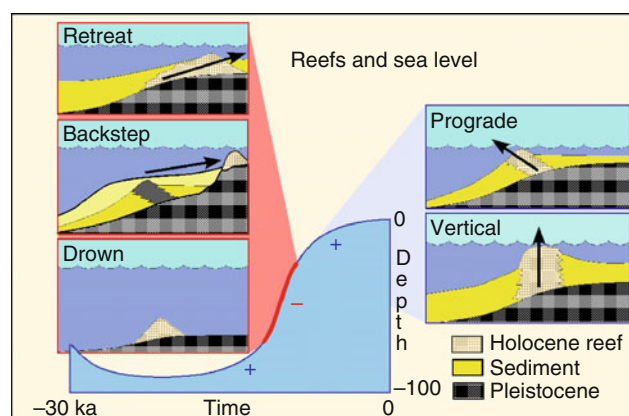
**Reef Drilling, Figure 7** (a) Underwater photograph of a modern Caribbean reef crest in the US Virgin Islands. The branching coral is *A. palmata*, which dominated Caribbean reef crests until near extirpation by disease in the 1980s. (b) Photograph of in-place, Pleistocene *A. palmata* on the south coast of Curacao, reflecting a similar environment. The live community in (a) sits within the “Branching-Coral Zone” on the modern reef crest; the fossil community in (b) is part of the “reef crest facies” or the “branching-coral facies,” suggesting a similar place on the reef 125,000 years ago (Photos by permission of the author).

same reef today. Because of the greater diversity in Pacific reefs, this comparison is less straightforward, but the same factors still control reef zonation. Most of the important modern coral species have been in existence since at least the early Quaternary, making these sorts of comparisons easier than is the case when dealing with older deposits. However, we can probably still be relatively confident in our comparisons as far back as the Triassic, when scleractinians corals developed their relationship with photosynthesizing zooxanthellae.

### Sea level versus reef accretion

As sea level rises, predictable shifts in community structure will occur, depending on the ability of reef building to keep pace (Neumann and Macintyre, 1985; Davies et al., 1985). When sea level is rising faster than the reef can aggrade, the reef will lag behind. This condition results in a gradual change toward species adapted to deeper water (primarily massive, fine-branching, and platy corals). If this pattern persists long enough, the reef will be abandoned once light levels become too low to support photosynthesis (i.e., a “give-up reef” of Neumann and Macintyre, 1985). This will also be reflected at a larger scale in (a) upslope retreat of the main reef facies, (b) backstepping (i.e., a landward shift in the locus of reef accretion) or (c) reef drowning (Figure 8).

Conversely, if sea level slows, as it has done for the past 6,000–7,000 years, some reefs that were being left behind will begin to “catch up” once the rate of sea-level rise slows to less than the reefs’ ability to build vertically. The sequence of corals will reflect progressively shallower water. If reef accretion and sea-level rise are roughly equal, water depth over the reef will remain constant. In this scenario, the “keep-up” reef will generally remain close to sea level and shallow-water species will dominate throughout the core (e.g., rapidly growing *Acropora palmata* in the Caribbean). In either case, facies geometry is usually dominated by vertical accretion (Figure 8). However, once sea level slows to the point that accommodation space is



**Reef Drilling, Figure 8** Reef-accretion patterns versus sea-level rise. When sea level is rising more slowly (i.e., near high- and low-stands: indicated by “+”), reefs will either build vertically when accretion and accommodation space are created nearly equally (catch-up or keep-up reefs of Neumann and Macintyre, 1985) or will prograde if reef building is the dominant factor in the equation (keep-up reefs). During intervals of rapid sea-level rise (“–”), reefs will “give up” by retreating upslope, backstepping (i.e., a new reef will form at a shallower and more landward site where conditions are appropriate for reef initiation), or simply being abandoned in place, depending on the rate of sea-level rise and the character of the underlying bathymetry. Thus, the facies geometry becomes a useful tool for understanding past patterns of sea-level change Hubbard (1997).

created more slowly than carbonate is produced to fill it, progradation will join upward aggradation and the reef crest will build “up-and-out.”

While simple models based on a vertical sequence of corals can provide a good conceptual framework for tying shifts in community structure to sea-level rise, these relationships can be complicated by changing oceanographic conditions. For example, a shift to a more vigorous wave climate can favor shallower-water species without



changing depth (Adey and Burke, 1977). Conversely, increased sedimentation or nutrient input can shift environmental boundaries upward (Acevedo et al., 1989).

On a larger scale, the patterns summarized in Figure 8 provide a generalized picture of changing facies geometry as rising sea level creates accommodations space and vertically accreting reefs try to fill it. However, a net landward shift of the reef crest over time does not preclude the downslope movement of detritus. Conversely, when the reef crest builds seaward as it tracks rising sea level, reef-derived materials can still move landward either within or between facies. In particular, as the reef builds close to sea level, small-scale transport patterns can vary markedly depending on reef geomorphology. After Hurricane Hugo, detrital transport was almost exclusively downslope and seaward where the Buck Island forereef sloped more steeply. However, where the forereef was gentler, material stripped from the face of the reef moved up and over the crest, resulting in 10 m of landward progradation of the reef flat in less than 24 h (Hubbard et al., 1991; Hubbard, 1992).

Thus, small-scale variations can exist within any larger-scale pattern. Nevertheless, the general picture provided by either changing corals or facies geometry revealed by cores still provides a reliable sense of the interaction of the larger reef system, the smaller-scale coral community, and rising (or falling) sea level.

### Environmental proxies

Physical, biological, and chemical proxies preserved within coral skeletons provide details of changing environmental conditions that can add to our larger-scale understanding of spatial and temporal changes in the reef environment over time. Smaller versions of the drilling systems designed to recover reef cores have been used to extract samples from living corals (Figure 1a). X-radiographs of corals reveal annual density bands that can be used as “calendars” by simply counting back from the live coral surface. When banding can be used to pinpoint specific time horizons within a coral, biochemical markers that are referenced to them can be used to hindcast a variety of oceanographic parameters. For example,  $^{18}\text{O}/^{16}\text{O}$  and Sr/Ca ratios reflect changes in temperature and salinity (Greer et al., 2009). Carbon isotopes can be used to assess the relative importance of photosynthesis at various times and at different places on the reef (Omata et al., 2005). Fluorescent bands in the same corals can be used to identify sudden increases in terrestrial sediment and nutrient input (Isdale, 1984). Even sediment can be trapped within a coral skeleton, providing direct evidence about the type and intensity of terrestrial input associated with natural or anthropogenically induced events in the past (Barnard et al., 1974; Cortes and Risk, 1985). Risk et al. (1987) have proposed that annual cycles of algal micro-boring may provide insight into the evolution of photosynthesis in corals throughout the Phanerozoic. Collectively, these windows into past oceanographic

conditions provide us with important information about short-term changes that cannot be discerned in the averaged record of larger-scale reef accretion.

### How reefs build

In addition to these insights into the history of specific reefs, important lessons have also been learned about the processes by which modern reefs build and how this compares to reefs formed throughout deep time. Ecological patterns respond to active processes that are, in turn, controlled by the edifice upon which they rest. Thus, corals owe their zonation to the depth gradients created as the end product of thousands of years of accretion as well as oceanographic process that are likewise affected by the large-scale morphology of the structural reef.

Until recently, it was assumed that reefs owe their rigidity and wave resistance to largely in-place and interlocking organisms. Calcification and coral growth were thought to exert the primary control on how fast a particular reef built. However, coring studies in the 1970s and 1980s provided a number of important, if counterintuitive, revelations. First, preserved coral skeletons only make up about a third of the material inside most Holocene reefs – and not all of these are preserved in growth position (Hubbard et al., 1998). The remainder of the reef interior consists of sediment, rubble, and open voids. Quantitative budgets that compare the “accretionary potential” of a reef (based on present-day abundance of corals and their rates of carbonate production) to what is actually preserved within that reef show that large quantities of carbonate are missing (e.g., Stearn and Scoffin, 1977; Land, 1979; Hubbard et al., 1990).

These findings encouraged a reassessment of the fundamental principles upon which our models of reef development are based. While corals and other skeletonizing organisms provide the building blocks for the reef, calcification is not the only – or even the primary – process that contributes to reef building. Over half of the carbonate produced by large skeletal organisms is reduced to sediment by organisms that graze on or bore into reef organisms. This weakens the initial structure and facilitates further physical and chemical breakdown, as well as the toppling and transport of coral colonies. The result is a structure that is as much detritus as it is in-place “reef-builders.” Were it not for the ubiquitous processes of cementation (probably mediated by bacteria – see Section) and encrustation (primarily by calcareous algae and other epibionts like foraminifera and bryozoans – see Section), this “garbage pile” would not be the rigid and wave-resistant structure that we call a coral reef.

Thus, paradigms that embrace the dominance of calcification in reef building have been replaced by alternative models in which calcification, bioerosion, cementation, and encrustation play roughly equal roles. A recent compilation of available reef-accretion data in Caribbean reefs has further decoupled initial calcification from net reef accretion (Hubbard, 2008). Despite the rapid decline in

**Reef Drilling, Table 1** Accretion rates within 5-m paleo-depth intervals. Note that no strong depth- or species-related pattern emerges from the data (Based on data from Hubbard 2008)

Mean accretion rate ( $\pm$  S.D.)

| Depth (m)      | N   | <i>A. palmata</i> | Massive         | Total           |
|----------------|-----|-------------------|-----------------|-----------------|
| 0–4.9          | 47  | $3.96 \pm 3.45$   | $2.53 \pm 1.65$ | $3.58 \pm 3.12$ |
| 5–9.9          | 40  | $4.33 \pm 3.00$   | $2.78 \pm 3.23$ | $3.79 \pm 3.13$ |
| 10–14.9        | 31  | $2.43 \pm 1.90$   | $3.19 \pm 2.45$ | $2.82 \pm 2.20$ |
| 15–19.9        | 7   | $2.09 \pm 0.17$   | $3.74 \pm 3.58$ | $3.27 \pm 3.04$ |
| 20–24.9        | 3   | 5.52 na           | $1.38 \pm 0.74$ | $2.76 \pm 2.45$ |
| <b>Overall</b> | 128 | $4.65 \pm 4.38$   | $3.17 \pm 3.28$ | $4.10 \pm 4.06$ |

light intensity, calcification and coral growth with increasing water depth, reef accretion appears to not follow the strong depth-related pattern that has been long assumed (Table 1). Reefs in shallow water and dominated by fast-growing branching corals built at rates that were statistically indistinguishable from reefs in deeper water and dominated by massive colonies. Although reefs appear to have accreted more rapidly, cores from the Great Barrier Reefs show a similar pattern (Davies et al., 1985; Hopley et al., 2007). If this is the result of decreasing rates of bioerosion with depth and the logical tendency for sediment to move downslope, then reef accretion might be thought of more as a sedimentological process than a biological one.

### Is what you see what you get?

Comparisons between modern and ancient reefs face numerous challenges, depending on the age of the reef and the way it is examined. In outcrops, a reasonably complete, three-dimensional picture is available. However, adequate temporal control can be difficult in reefs older than the Quaternary. We can assign a general age to an older reef, but it is difficult to accurately date individual corals and, therefore, to assign rates to what we see in the rock record.

As we go further back in time, problems of changing taxa are introduced as the march of evolution becomes increasingly significant. Within a Holocene reef, organisms are the same as those on the surface. Quaternary reefs were built by organisms that are either still in existence or can be easily traced to extant species. But, as we go further back in time, this gets increasingly difficult. For example, 340 million years ago reefs were built by stromatoporoids that probably responded differently than corals to depth gradients and variations in physical processes.

### The taphonomic filter

Even in a well-exposed outcrop, myriad processes have been at work that create differences between what actually existed on the sea floor in the past and what is ultimately preserved in a fossil reef. Collectively referred to as taphonomy, these issues are related to everything that happened to an organism from the time it died to when it was

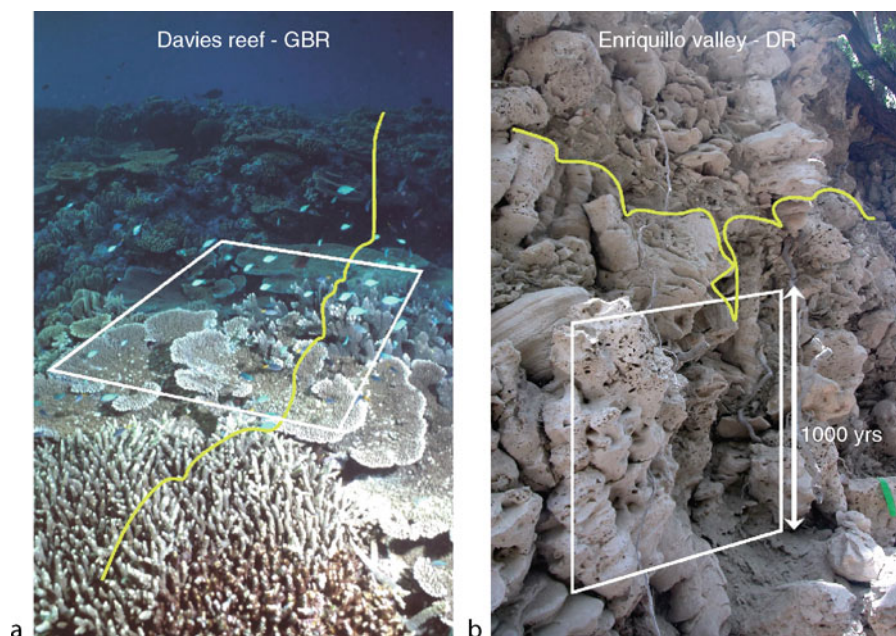
(or was not) fossilized. Obviously, soft-bodied organisms are preserved only in unusual circumstances. Fragile skeletons (e.g., platy corals) will break down more easily than branching ones, which are in turn less preservable than massive colonies. Rare taxa are less likely preserved than more abundant ones. Finally, postmortem disintegration and transport can move smaller fragments considerable distances from their initial environment, especially where slopes are high or storms are frequent. If we add later diagenetic processes to the mix, fidelity to the original community structure is even further compromised. These problems are greatly moderated in reefs, which contain so many robust skeletal taxa. Nevertheless, diversity may still be reduced by up to 90% as reef organisms pass through the “taphonomic filter.”

### Time averaging

Anyone who has spent much time on a reef appreciates the spatial and temporal variability that exists within even a small area. If we scale this up to the millennia over which reefs build, a seemingly infinite combination of species might occupy a particular spot on the reef over its lifetime. The result is a fossil record in which a sampling of corals over even a small area or a short length of core can represent huge time spans. Because of this “time averaging,” it can be difficult to separate changes in species related to environmental variability from those that simply reflect the decadal changes that normally occur on any reef. Even if we use what appear to be identical methods, the results may not be comparable. For example, a quadrat on a reef (Figure 9a) provides a detailed accounting of species abundance and diversity at one place and at one instance in time. In contrast, that same quadrat placed on a rock face (Figure 9b) will contain an amalgam of the corals that were preserved over perhaps a millennium or longer. Similarly, a transect survey over a live reef (e.g., the irregular line in Figure 8a) records spatial variability, and it is easy to determine which corals are live or dead at that instant. Even if we were able to somehow identify a similar time-equivalent surface within an outcrop (Figure 9b), it is difficult to determine which corals beneath that imaginary line were alive or dead at the same time. If we further limit ourselves to the vertical sampling provided by a core through the reef, these problems increase.

### Why is reef zonation preserved at all?

Given all the ways that the original community structure can be modified before burial and the myriad issues of selective preservation over long intervals of time, one might wonder how reef zonation is ever preserved. While in-place corals may not make up the majority of the reef as was previously thought, those colonies that are left behind still provide important information about the environment in which they lived and died. Also most larger colonies that are toppled do not move significant distances from their original location and will probably end up in or near their original environment, even if they are not “in place,”



**Reef Drilling, Figure 9** Comparison of quadrats (*squares*) and transects (*irregular lines*) on the modern reef surface and along fossil-reef outcrops. The quadrat on Davies Reef in the Great Barrier Reef (a) tallies what exists in that square meter at a particular time. In contrast, that same quadrat placed on the Holocene reef wall in the Dominican Republic (b) will contain corals that existed over some time span, probably on the order of 1,000–4,000 years. Similarly, the transect across the reef in (a) provides an accurate accounting of organisms along a depth gradient, and it is easy to differentiate live and dead corals to obtain an accurate measure of coral cover. Even along the timeline created by storm burial in the DR fossil reef (b), it is difficult to tell which corals were alive or dead at an instant in time (Photos by permission of the author).

they are still *in situ*. Sediment and rubble trickles down inside the reef where it is deposited, or it is transported to some other place – either on the reef, or far away if storms or steep slopes come into play. Nevertheless, enough of the community structure is preserved to allow most of the large-scale inferences that we commonly make from outcrops and cores.

### Potential coring artifacts

In addition to issues of selective loss and preservation, a number of potential problems that are specific to the coring process must also be kept in mind. The rotating drill bit can fragment more fragile samples and, combined with water flow through the core barrel, it can push smaller samples out of the way. Sediment recovery is virtually impossible. Slower rotation speeds, maintenance of constant pressure on the drill bit (i.e., not letting it jump up and down, especially in rubble-dominated intervals), and minimizing water flow can greatly reduce these problems, but only rarely can they be totally eliminated.

Slowly augering or pounding thin-walled core barrels by hand (without water flow) can reduce or even eliminate the loss of smaller samples, rubble, and sediment (Dardeau et al., 2000). However, this process is tedious and is able to penetrate only 2–3 m under ideal conditions in unconsolidated, finely branching corals. Pneumatic coring has been used to drive a core into the reef by

percussion rather than by rotation. Recovery is excellent and selective losses are minimized. However, this method is limited to shallow water where air-pressure losses are minimal and safe handling of large pneumatic equipment is possible. It has been proposed that using larger core barrels (>15 cm) might improve recovery. However, this has not been systematically tested, and anecdotal observations argue against it, except when compared to very small core barrels ( $\leq 5$  cm) where high loss rates are known to occur.

### Accurate core logging

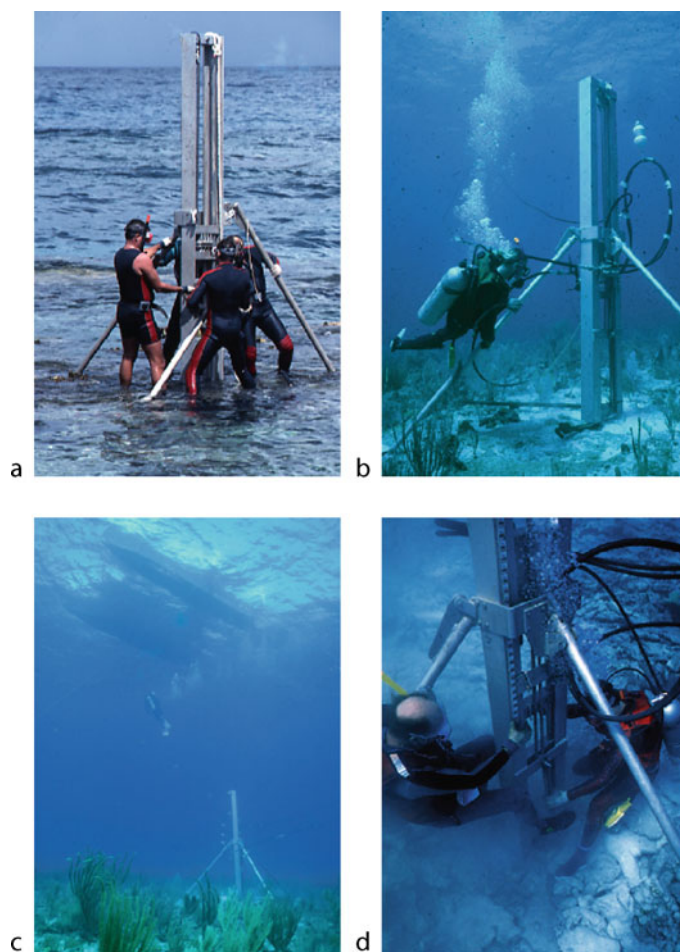
Use of a traditional tripod can make it hard to reliably determine the exact vertical position of a recovered sample, even within a single 1.5-m core interval. Reefs are typically very porous, and cavities can be open or filled with sediment and rubble derived from biological breakdown of the reef. During coring, the lifting cable is typically left slack to make sure that drilling progress is unimpeded. When the unsupported drill string encounters an open void, it free-falls until it either reaches the bottom of the hole or the slack in the lifting cable is taken up. In this scenario, the bottom of the void can be easily determined by measuring the length of the drill string in the hole at that point. However, unless the operators have been exceedingly vigilant, the top of the void will be based on the collective recollection of the stunned crew regarding where the rig was just before it plummeted. When a core



barrel is recovered, it is often less than half-full, owing to the porous nature of the substrate. Where the core interval ends in a continuous and solid substrate, the position of that single piece can be accurately determined. However detailed measurements for small samples and interspersed voids are rare, and placing the numerous small pieces in an accurate vertical context is often difficult. This can affect calculations of reef-accretion rates.

Resolving this issue requires a drilling system in which the drill string is positively controlled as coring proceeds. In one such system, an adjustable tripod is incorporated into a rigid frame that provides stability (Figure 10).

Rather than being loosely hung on a wire, the drill motor travels along two rails, and is both raised and lowered by a chain drive that precisely maintains the position of the drill string throughout the coring process (Figure 10d). The crank handle that operates the chain drive maintains constant pressure on the bit throughout drilling. Vibrations caused by the drill bit interacting with the substrate are passed up the drill string, along the chain drive and into the drive handle. These vibrations, plus the rate of penetration in response to a reasonably steady downward pressure, provide tactile feedback from even small changes in the nature of the substrate. An open void is instantly



**Reef Drilling, Figure 10** Photographs of the SCARID drilling system. (a) Drilling frame deployed along the shallow reef crest in Buck Island Underwater National Monument, US Virgin Islands. The operator (*left*) uses hydraulic power to rotate the drill string, control water flow, and raise and lower the messenger that is used to recover the inner core barrel. (b) Drill frame deployed in 13 m of water on Lang Bank, St. Croix, US Virgin Islands. The drill string is to the right of the coring tower. Controls are located on the backside near the diver. Water and power come through hoses from the surface. (c) Drill on the bottom beneath its support catamaran. The drill and the water pump are powered by a 17-hp diesel on the platform. Easy launch and recovery are facilitated by the open section in the center of the catamaran. The system has been used on modest vessels of opportunity, and requires only an open deck on the order of 4 m  $\times$  4 m. (d) Divers operating the SCARID drilling system. The diver on the right is maintaining drilling pressure on the core barrel using a handle attached to the stainless steel drive chain. Note the metric scale on the left side of the drill frame. This provides a convenient and accurate reference for the vertical position of the drill string in the hole. The operator uses predetermined hand signals to indicate drilling character to the back-up diver who records this information along with the position at which each change occurs (Photos by permission of the author).

registered through the drive handle, and low gearing makes it easy to immediately stop any free fall. Sandy intervals are rapidly traversed, but with easily discerned resistance. In rubble intervals, the feel of the bit bouncing against the irregular and mobile surface is unmistakable. Solid intervals require increased pressure that is proportional to the resistance of the substrate being cored (primarily reflecting coral density).

The result is an ability to sense and locate even small changes in the reef interior. Each time the drilling character changes, the position of the drill motor is referenced to a metric scale mounted on the drilling frame (Figure 10d). Using these notes and the lengths of the recovered samples, a log can be created that accurately locates each sample and adequately interprets the unrecovered intervals in between (Figure 3c). Early testing involved trying to match the number of solid samples in a core barrel (and their lengths) to the intervals recorded in the drilling notes. These predictions were usually accurate to within 5% of what was actually found when the inner barrel was emptied.

The main disadvantage of this system and other sophisticated coring systems is the greater logistical complexity associated with them. Even small jack-up rigs (e.g., Figure 5c) need to be towed to the site and require sufficient water depth over the reef to float them into place. Larger traditional systems (e.g., Figure 5a) are limited to dry land or to water depths shallow enough to allow easy access and little potential for wave overtopping. Drilling frames like the one used in the submersible coring apparatus for remote insular drilling (*SCARID*) system can be used in all environments (Figure 10), but can still be more cumbersome and require better trained scientist/divers to deploy and operate them. However, the increased predictability (nearly all cores taken with larger systems penetrate through the entire Holocene section and little time is lost getting stuck in the hole) can result in significant time offsets. Once in place, the additional weight of larger drills translates into greater stability and a significantly increased level of accuracy with respect to sample location and core logging. Considering the funds required to mount a field operation and analyze the recovered samples, the increased cost of deploying a moderately larger system is probably less of an issue than assembling a crew that is adequately trained to take advantage of its positive attributes.

### The "Two-Inch Outcrop"

Even with the largest and most reliable drilling system, cores provide a limited picture of the reef interior. The myriad issues discussed above notwithstanding, a single core is the equivalent of a 5–10-cm wide outcrop that provides a single, vertical characterization of the reef interior. However, multiple cores that are accurately located along a well-constrained transect can provide a good three-dimensional picture as long as adequate vertical control of sample positions and sufficient radiometric dates are possible (Figure 6). The central question is always,

"How many cores are enough?" Using uniquely exposed Holocene reefs in the western Dominican Republic, detailed vertical transects were measured to create "virtual cores." Each "virtual core" was located both vertically and horizontally using differential Global Positioning System (GPS) measurements and laser surveys. Radiocarbon dating temporally constrained the patterns of reef development. Changes in paleo-water depth were computed using each sample's vertical position, its age, and the most-accepted Caribbean sea-level curve (the original Lighty et al., 1982) curve adjusted by using accepted isotopic corrections (e.g., Hubbard et al., 2000; Toscano and Macintyre, 2003; Hubbard et al., 2005). Approximately five evenly spaced "virtual cores" provided a good representation of the large-scale facies patterns that were identified within the full exposure of the 450-m long outcrop. Furthermore, changing depositional patterns seen in the "virtual cores" allowed a general characterization of transgression versus regression across the entire outcrop.

What was consistently missing from the core record, even when more "virtual cores" were added, was an accurate accounting of the full range of species present in the outcrop. Over 25 coral species and 50 mollusc species were identified in the outcrop, but only a handful of coral taxa and virtually no molluscs were sampled by any combination of "virtual cores." Nevertheless, the temporal and spatial changes in major species were still adequate to accurately characterize larger-scale paleoenvironments (i.e., zonation) in the outcrop. Overall reef morphology, and the relationship between facies changes and the rate of sea-level rise were likewise reasonably characterized. Finally, small-scale fabrics within individual samples (e.g., bioerosion, cementation, and encrustation) and their relationship to larger-scale patterns within the reef structure were reasonably constrained. In short, while a detailed characterization of coral-community structure may have been lacking, the larger picture of zonation and shifts of major corals in response to physical-oceanographic processes and sea level still emerged. Thus, despite all the pitfalls of fickle preservation and time averaging, the important relationships that are of interest to geologists were still discernible.

### Summary

The interiors of modern reefs are rarely exposed, leaving few options for collecting information on past reef morphology, internal structure, and history. Well-documented issues with preferential preservation make it obvious that the reef we find preserved is different than the reef that actually existed in the distant past. Issues of recovery and precise positioning of samples add to these problems. Nevertheless, coring remains as our most valuable tool for gaining access to the interiors of modern coral reefs around the world. Despite the known problems, cores have provided a realistic characterization of the primary reef-builders and the general temporal framework over which they have contributed to the rigid and

wave-resistant structures that support today's coral-reef community. Comparisons with continuous exposures indicate that as few as three to five cores can provide a reasonable picture of fossil zonation as well as the pattern of reef building in response to changes in physical oceanography and the rate of sea-level rise and fall. Proxy data from individual corals within a core can provide important information on short-term variability in past ocean conditions. Thus, we can use observations and measurements on modern reefs to better understand the complex relationship between process and product in the past. Applying all these to our cores, we have been able to reconstruct patterns of reef accretion as rising sea level flooded major shelf areas around the world, and have come to understand how the reefs that followed responded to changing physiochemical processes and sea-level rise when "we were doing nothing." The models developed using this information have helped us to tie reef organisms to the structures that they presently occupy. If we remain mindful of the problems associated with interpreting fossil assemblages, we should be able to apply the lessons of reefs operating before major human influence to questions about future changes and suggest sound management strategies that take into account both natural change and the effect of processes that operate over time intervals longer than the attention span of a typical politician, the funding cycle of an individual research project, the life of a scientist, or even the disciplines of biology and geology.

## Acknowledgments

The greatest and most obvious debt is to the researchers who have wrestled with the practical and intellectual problems associated with sampling the interiors of Holocene reefs. Starting with researchers from the Smithsonian Institution and growing into a community of researchers as diverse as the reefs they study, a suite of drilling strategies have evolved that balance simplicity and depth of recovery; the list is too long for adequate individual acknowledgment of the individuals that have made our way easier. Studies by the author that contributed to the information provided in this chapter were funded by the National Science Foundation (St. Croix cores), the Sea Grant and Undersea Research Programs of the National Oceanic, and Atmospheric Administration (fabrication of the SCARID drilling system; cores in Salt River, St. Croix; Puerto Rico and the Florida Keys), the US National Park Service (cores in Buck Island Underwater National Monument), the National Institute for Global Environmental Change (Puerto Rico cores), and the Petroleum Research Fund of the American Chemical Society (Dominican Republic studies).

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[Bahamas](#)  
[Barbados](#)  
[Belize Barrier and Atoll Reefs](#)  
[Bermuda](#)  
[Brazil, Coral Reefs](#)  
[Florida Keys](#)  
[Meltwater Pulses](#)  
[Reef Classification, Response to Sea Level Rise](#)  
[Submerged Reefs](#)  
[Western Atlantic/Caribbean, Coral Reefs](#)  
[West Indian Coral Reef Classification](#)

## REEF FLATS

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## Synonyms

Coral-dominated reef flat; Rubble-dominated reef flat

## Definition

Reef flats are the most recent expression of coral reef (see Chapter [Coral Reef, Definition](#)) growth at sea level. There are two forms of reef flats: (1) coral-dominated

and (2) rubble-dominated. In each case, they represent the growth of reefs in the ambient energy conditions as the growing reef approaches the sea-level environment.

### Example of reef flats

One Tree Reef ( $23^{\circ}30'S$ ,  $152^{\circ}06'E$ ) in the Capricorn–Bunker Group in the southern Great Barrier Reef (see Chapter *Great Barrier Reef: Origin, Evolution, and Modern Development*) (Figure 1b) is an example of both forms of reef flats. It is subjected to prevailing trade winds, predominantly from the southeast (Figure 1c), resulting in the formation of reef flat features common to reefs throughout the world. It currently represents one of the largest modern databases in the Great Barrier Reef (Davies, 1983). It is this reef that is used as an example of the development of both coral- and rubble-dominated reef flats.

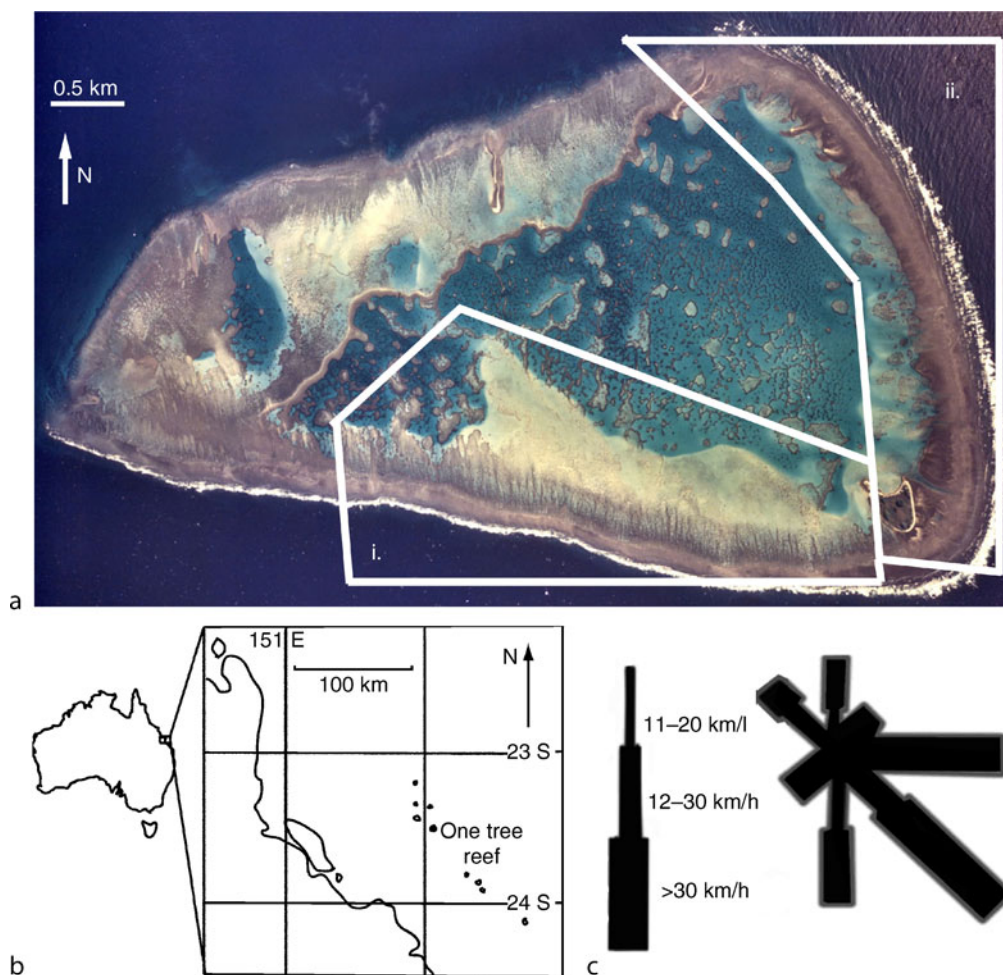
### Coral-dominated reef flats

The southern reef flat of One Tree Reef is dominated by live coral growth (Figure 1a-i). It is composed of six distinct morphobiological zones; algal flat, rubble band, fused coral windrows, unfused coral windrows, coral patches, and sand flat. Wide algal flats, reef flat windrows, and prograding sand bodies collectively are common sea-level growth signatures on high-energy reefs (Davies et al., 1976; Jell and Flood, 1978; Davies and Marshall, 1979). This zonation is commonly found on high-energy reefs globally.

### Components of the coral-dominated reef flat

#### Algal flat

The algal flat (see Chapter *Algal Rims*) is the most windward zone. It is comprised of epilithic layers of calcareous



**Reef Flats, Figure 1** (a) Aerial photograph of One Tree Reef (i) the southern coral-dominated reef flat (ii) the eastern rubble-dominated reef flat; (b) location of One Tree Reef; (c) wind-rose showing predominant southeasterly winds.

algae and mats of filamentous turf algae (see Chapter *Algae, Turf*) with an endofauna comprised mainly of benthic foraminifera (see Chapter *Foraminifera*). The surface slopes towards the reef front (see Chapter *Forereef/Reef Front*) in a series of laterally discontinuous but distinct algal terracettes.

### Rubble band

Leeward of the algal flat is a thin rubble band (see Chapter *Boulder Zone/Ramparts*) consisting of coral rubble and algae which accumulates on the inner edge of the algal flat. It is widest at the southeastern end, narrowing westward. The coral rubble is largely composed of dead and fragmented plate, branching and massive growth forms.

### Coral windrows

Leeward of the rubble band is the coral windrow zone, occupying much of the upper surface of the southern reef flat (Figure 2). Windrows are elongated structures of coral framework, separated by narrow sandy channels up to 10 m in width. Windrows typically have a solid pavement surface of coral and coralline algae (see Chapter *Algae, Coralline*), where growth has reached the mean low-tide level. The framework of the windrows is composed of robust branching and massive coral growth forms and is consolidated by smaller coral growth forms and coralline algae.

1. Fused coral windrows: Adjacent to the rubble zone, the channels between the windrows are filled with rubble, sediment, and live coral growth such that adjacent windrows fuse together, creating the fused windrow zone.
2. Unfused coral windrows: Leeward of the fused windrow zone are unfused windrows, extending toward the sand flat. This is easily the most discernible zone, comprising the main coral flat.



Reef Flats, Figure 2 Coral-dominated reef flat: coral windrow.

### Coral composition of the coral windrows

Five dominant scleractinian (see Chapter *Scleractinia, Evolution and Taxonomy*) coral growth forms comprise the coral-dominated reef flat at One Tree Reef; branching, massive, encrusting, laminar, and free-living. The distribution of these forms changes both transversally along the length of the windrows from windward to leeward and longshore across the reef flat from southeastern windrows to southwestern windrows.

Longshore variations include the following: (1) massive and encrusting corals dominating the southeastern windrows, while branching and encrusting forms dominate the southwestern windrows; (2) massive and branching corals display an inverse relationship whereby the percentage cover of branching corals increases from the southeastern windrows to the southwestern windrows, while massive corals decrease towards the southwestern windrows; (3) branching coral cover is greatest in the leeward section of the southeastern windrows and the windward section of the southwestern windrows; (4) branching *Acropora* species (see Chapter *Acropora*) count increases by a factor of +3 from the southeastern windrows to the southwestern windrows.

The windrows themselves experience transverse variations in the distribution of the dominant coral growth forms cover. Using the southeastern windrows as a specific example, the windward section of the windrows is dominated primarily by massive corals and secondarily by robust low-branching forms. The leeward section of the windrows is dominated primarily by branching corals and secondarily by massive coral forms.

### Coral patches

The coral patches zone lies leeward of the coral windrows and consists of shallow patches of coral and algae that form discontinuous extensions of the windrows onto and across the sand flat. Coral patches range in size from 2 m to less than 1 m in diameter.

### Sand flat

The sand flat occurs leeward of the coral patches zone, sloping into the lagoon (see Chapter *Lagoons*). It is comprised of medium to coarse coral sand derived from all windward environments (see Chapter *Reef Flats*), coralline algae, foraminifera, molluscs (see Chapter *Molluscs*), bryozoans (see Chapter *Bryozoa*), and sponges (Davies, 1977; Davies and Kinsey, 1977) (see Chapter *Reefal Sediments*).

### Formation of the coral-dominated reef flat

Reefs are subjected to prevailing energy conditions and, in the case of One Tree Reef, predominantly from the southeast (Figure 1c). Therefore, the area most affected by this energy is the southeastern corner of the reef, with energy diminishing transversally toward the lagoon, as well as longshore down the length of the southern coral-dominated flat.



This southeastern corner is also the highest measured point on the coral-dominated reef flat, sloping down both transversally toward the lagoon as well as longshore down the length of the reef flat. Together, the height of the reef substrate and the energy regime compose the main physical and environmental parameters influencing the development of the coral-dominated reef flat. Combining the two, the southeastern corner becomes the shallowest, highest energy point on the reef, with both height and energy dissipating in transverse and longshore directions. The consequence is that higher energy propagates further across the reef at the southeastern corner.

It is reasonably well established that corals and other benthic organisms distribute themselves on the reef flat in response to the ambient environmental parameters (see Chapter *Corals: Environmental Controls on Growth*), including the dominant physical processes to which they are exposed (Done, 1982; Sebens and Done, 1992; Merks et al., 2003; Kaandorp et al., 2005; Kruszynski et al., 2007). While morphologic and biologic variability of reefs involves a plexus of interactions between chemical, biological, and physical processes, wave energy is recognized in many studies as one of the most important controls of coral reef growth and subsequent development at sea level (Roberts, 1974; Done, 1982, 1983; Dollar, 1982; Storlazzi et al., 2005; Kench and Brander, 2006). The southern coral-dominated reef flat of One Tree Reef expresses the effects of these parameters in both transverse and longshore directions, with a number of possible relationships: (1) high-energy and a high-reef surface creates an area dominated primarily by massive and encrusting corals with some robust, low branching on the most windward areas; (2) lower or less energy and a lower reef surface creates an area dominated primarily by branching corals in the leeward section of the most exposed windrows with some massive forms; and (3) the lowest energy and surface creates an area of high diversity (of *Acropora* species) in the windward areas.

### Stages of development

Drill cores reveal that the coral-dominated reef flat is composed of an initial stage of massive coral growth in water depths of approximately 10 m, followed by mixed massive and branching biofacies, with branching corals dominating as the reef approaches sea level (immediately below the current windrow zone) (Marshall and Davies, 1982; Davies and Hopley, 1983). Criteria used for identifying the in situ nature of drill cores include (1) algal crusts atop coral pieces and down the side of solid coral pieces (identical relations are seen on the coral flat today), (2) continuity of long coral pieces in the core, (3) the disposition of adjacent fauna and flora, (4) geopetal cavities, (5) the disposition of crypto fauna beneath or within cavities, and (6) the direction of growth of cyanobacterial finger-like growths within cavities in or on corals. No material was selected for dating if it had been reboored or from the core-catcher.

The development of the coral-dominated reef flat at sea level on One Tree Reef occurs in three stages: formation of aligned windrows and development of the sand flat, formation of the windward fusion zone and the formation of patches, and smothering of the lagoonal micro atolls (see Chapter *Microatoll*) by sand.

Coral windrows are comprised of framework constructors and framework fillers, and are the direct result of the interactions between the two to create a consolidated matrix. Both use the available living space, with one constructing the basic framework while the other consolidating this framework matrix by growing in the secondary environments created by the constructors. The living space created by the primary framework corals provides stability and support by direct contact for such infill species. The strength and physical complexity of this matrix of corals is cemented by coralline algal infill, with additional consolidation occurring with the incorporation of sediment within the coral framework.

Framework constructors are primarily branching and massive corals. Framework fillers are frequently fragile branching forms and include all growth forms, with branching, massive, and encrusting forms dominating. Some coral species may be both framework constructors and fillers depending on their position on the reef flat. For example, *Favites* is a massive framework constructor in the windward section of the windrows, while it is a filler in the leeward section of the same windrows. As the coral framework is established and approaches sea level, and therefore is increasingly affected by the prevailing energy, the corals begin to develop aligned windrows parallel to the dominant flow direction. The windrows in turn diversify the physical conditions in which they grow in relation to gradients in water flow velocity creating biological zonation of the corals (Stoddart 1969; Geister, 1977; Dollar, 1982; Done, 1983; Massel and Done 1993; Rogers, 1993; Storlazzi et al., 2005; Kruszynski et al., 2007).

Simultaneous to the formation of coral windrows is the development of the sand flat. Sand sourced from the coral windrows, produced mostly through bioerosion (see Chapter *Bioerosion*) and physical erosion, is transported leeward by the prevailing energy. This leeward prograding of the sand flat into the lagoon facilitates the lateral leeward expansion of the reef flat. As the sand flat grows, it provides a substrate of suitable depth on which corals can colonize, allowing coral growth to continue in a leeward direction. The rate of this prograding is predicted to decrease as the sand flat moves further away from the dominant sediment source (Davies, 1983).

After the establishment of the coral windrow matrix and sand flat, the process of windrow fusion occurs. The fused zone forms in the windward section of the windrows (most prominently in the southeastern windrows) when the windrow structure has grown to the mean low-tide level and formed a hard surface on the top surface of the structure of predominantly coral and calcareous coralline algae, thereby limiting further vertical growth without

a change in sea level. As a result, the corals grow laterally along the sides of the windrows, often perpendicular to the dominant flow direction, closing in the channel between windrows, resulting in “fusion” of adjacent windrows, obliterating the windrow structure along its length from windward to leeward. After fusion, the hard coral and algal surface is exposed at low tide resulting in its breakdown to rubble. As this process moves leeward, so too does the calcareous algae of the algal flat.

While the coral windrows are fusing in the windward section, the coral patches zone extends the windrows leeward across the sand flat. The initial stage of patch development occurs when storm-transported coral fragments (largely branching species) are transported leeward of the windrow onto the sand flat. These fragments either die or regenerate, becoming a monospecific colony. Small colonies of framework constructors (and few fillers) grow on the dead coral fragments either through further fragment transportation or planulae. As branching corals are often the first to increase their bottom coverage in such nonspace-limited stands and their growth rates are significantly higher than that of planulae-dependent massive corals (Sebens and Done, 1992), branching corals dominate these colonies. These colonies grow over the sand as low patches, touching the sand only in point contact. The patches are eventually consolidated when filler corals, such as *Goniopora* and *Favites*, are added to the framework matrix. These patches then expand through both vertical and horizontal growth until adjacent coral patches fuse together and to the main windrow structure, thereby extending the coral windrows leeward across the sand flat.

Smothering of the lagoonal micro atolls by the leeward extension of the sand flat occurs when lagoonal sands are transported leeward into the lagoon, gradually covering the lagoonal micro atolls. Corals are unable to survive such smothering, and as a result, the lagoonal micro atolls die and are colonized by algae.

### Rubble-dominated reef flats

The eastern reef flat at One Tree Reef (Figure 1a-ii) is a rubble-dominated reef flat, nearly 4.5 km long and up to 0.5 km wide, containing an estimated 14 million tons of rubble (see Chapter *Shingle Ridges*). Drilling has shown a maximum depth of 8 m of rubble material (Davies and Marshall, 1979; Davies and Hopley 1983). It is highest along the lagoonal edge and lowest at the junction with the algal flat. The difference in height between the two averages 40 cm. The boundary with the lagoon is either straight or indented with spurs and gutters. Supratidal islands occur on the intertidal rim in the south and in the north. The islands are comprised of successive rubble storm ridges. The upper surface of the rubble flat is strewn with rubble spurs, all of which indicate derivation from the east and southeast. New rubble spurs are habitually comprised of stick coral rubble above larger massive and plate corals, the whole exhibiting a decrease in grain size. The long axis of most clasts of stick rubble

is at right angles to the direction of movement, suggesting turbulent flow (Gourlay, 1988; Nott, 2003). The material forming the rubble surface commonly exhibits imbrication of plate and massive corals and the alignment of stick coral fragments. The rubble flat shows a clear zonation: massive and plate rubble weighing between 10 and 20 kg dominate the outer flat adjacent to the algal flat (Figure 3); plate and massive rubble weighing between 5 and 10 kg and minor branching forms dominate the mid-flat; and stick rubble and some plate rubble dominate the inner rubble flat adjacent to the lagoon. Often, the stick rubble forms linear mounds on the very edge of the lagoon.

### Formation of the rubble-dominated reef flat

The rubble on the eastern reef flat at One Tree is clearly derived, with no live coral growth occurring currently on the flat (see Chapter *Corals: Biology and Skeletal Deposition*). Imbrication, aligned stick rubble on spurs, storm ridges on islands, and the zonation of the rubble-dominated reef flat itself indicate that the material is derived from the windward reef front below mean low water. Analysis of coral species from both reef front (from mean low water down to depths of 15 m) and reef flat rubble confirms that the same species are present in both environments; indeed, coral rubble identical to that on the flat lies in the grooves between the spurs. It is concluded therefore that live coral is broken on the reef front, accumulates in situ, and is picked up and transported up on to the rubble flat. However, the evidence on the rubble flat itself indicates that transport of material may occur as two separate but related processes: (1) the initial dump of a mixture of material on the outer flat; and (2) the physical separation and sorting of that material on the rubble flat itself. These processes are clearly physical, a statement of which lies in the record of energy impinging on the reef. At One Tree Reef, a summary of this record is shown in Table 1. Energy is a function of wind (velocity and direction) and sea state (wave height, wavelength, and period) and can



Reef Flats, Figure 3 Rubble-dominated reef flat: outer rubble flat.

**Reef Flats, Table 1** Winds, sea state, and physical energy in the system in deep and shallow water. It should be noted that the energy in the system increases by 1.5 orders from low to high energy

| Energy class | Beaufort scale                | Sea state | Wave height (m) | Wind velocity (km/h) | Wave Period (s) | Wave length (m)    | Deep water wave energy (N m) | Shallow water wave energy (N m) |
|--------------|-------------------------------|-----------|-----------------|----------------------|-----------------|--------------------|------------------------------|---------------------------------|
| Low          | Calm to moderate breeze       | 0–3       | 0–1             | <1 to 20–29          | 0–4             | 0–20               | 277–1,100                    | 135–550                         |
| Intermediate | Fresh breeze to strong breeze | 4–5       | 2–3.5           | 30–39 to 40–50       | 5 to 5–7        | 30 to 35–50        | 1,100–3,600                  | 550– 3,600                      |
| High         | Near gale to storm            | 6–9       | 5–14            | 52–61 to 89–102      | 7–9 to 15–18    | 60–90 to 849–1,091 | 7,500–24,300                 | 3,600–12,000                    |
| Extreme      | Violent storm                 | 10        | >15             | >94                  | 20              |                    | >30,000                      | Extreme                         |

**Reef Flats, Table 2** Proposed relationships between energy and construction/destruction on the rubble reef flat

| Energy class | Tidal height | Likely processes                                                            | Likely products                                                            |
|--------------|--------------|-----------------------------------------------------------------------------|----------------------------------------------------------------------------|
| Low          | Low          | Oscillating waves top 5 m                                                   | Sand entrained on front                                                    |
| Intermediate | Low          | High<br>Refracted waves                                                     | Sand transported to sand flat. Sorting of stick rubble                     |
|              |              | High<br>Wave destruction of branching coral forms                           | Accumulation of rubble on reef front                                       |
| High         | Low          | High<br>Refracted wave transport                                            | Stick rubble transported to form rubble flat spurs                         |
|              |              | High<br>Major wave destruction of massive and plate corals                  | Stick rubble transported into the lagoon                                   |
| Extreme      | Low          | High<br>Major wave destruction of massive and plate corals                  | Massive and plate corals separated on the reef flat                        |
|              |              | High<br>Massive destruction of reef front                                   | Imbrication of plate rubble                                                |
|              |              | High<br>Continued destruction. Production of rubble transported to reef top | Chaotic rubble on the reef front                                           |
|              |              |                                                                             | Unsorted dumping of rubble on reef flat. Dumping of rubble into the lagoon |

be calculated quantitatively (Table 1). Wind strength and sea state are strongly related. Using these parameters and calculating energy within the system, four energy states can be defined in the surrounding ocean (Table 2) and summarized as follows:

- Low energy – calm airs to light breezes – total energy of 277–550 N m
- Intermediate energy – fresh to strong breezes – total energy of 1,100–3,600 N m (a three times increase in energy levels over stage 1)
- High energy – near gale to storm – total energy of 3,500–24,300 N m (a 3–10 times increase in energy levels over stage 2)
- Extreme energy – violent storm – total energy in excess of 30,000 N m (a total of 2 times minimum increase in energy levels)

Note that in moving from stage 1 to stage 3 (historically a common annual phenomenon), energy in the system increases by 1.5 orders of magnitude. The historical record of wind and sea state therefore defines the length and frequency of the energy windows which have impinged on

One Tree Reef and reefs like it. When the deep water wave energy approaches a reef edge, a shoaling occurs in approximately 30 m of water (see Chapter *Reef Front Wave Energy*). The energy of the wave moving forward is approximately half of the energy of the deep water wave, the rest of which dissipates against the fore-reef (see Chapter *Wave Shoaling and Refraction, Waves and Wave-Driven Currents* and *Wave Set-Up*). How the forward moving energy is used is then a function of whether it is totally expended on the reef front or whether it is expended across the reef in total; this is dependent on the tides (see Chapter *Tidal Effects on Coral Reefs*). The tides in the Great Barrier Reef region are semi-diurnal and their height varies depending on springs/neaps and solstice/equinoctial time frames with a maximum tidal range at One Tree Reef of 0–3.5 m. In any assessment of energy within the system, therefore, it is important to note that reef flats are periodically covered by nearly 3.5 m of water, while at other times the upper reef fronts and reef flats are exposed. In the context of distribution of energy, therefore, low tides are periods when energy is concentrated almost entirely on the reef front, while high tide periods define



energy distributed across the whole reef system (not equally). In terms of the processes recognized qualitatively as occurring in producing the rubble flat, i.e., breakage, storage, transport and dumping on the outer rubble flat, and sorting on the flat, coupling the energy levels to windows of opportunity (high and low tides) defines when the major processes occur (Table 2).

The frequency of the energy levels reported in Table 1 and therefore the processes described in Table 2 can be gauged from a historical database of wind and tide data. At One Tree Reef, this shows relatively low energy conditions persisting for 270–352 days a year for the past 48 years, with 1960 and 1988 representing intermediate and high energy spikes in this generally low-energy record. However, intermediate- and high-energy events occur every year to some degree, and in nearly all cases, that energy is directed at the reefs from the east to south-east quadrants. In addition, these blow particularly strongly during the January–June period and especially during the equinox and solstice spring tides. The processes and products that comprise the rubble flats therefore occur largely in these periods but mainly in the March–April period.

## Conclusions

Reef flats represent the most recent growth at sea level of modern coral reefs. They are recognized globally as two forms: (1) coral-dominated; and (2) rubble-dominated. Coral-dominated reef flats reflect the interaction between the biotic communities and the energy characteristics of the environment, creating distinct zonations. The coral flat is divided into fused windrows, unfused windrows, and patches. Coral growth forms vary transversally across and longshore the coral flat. Both variations reflect a decrease in reef height and wave energy.

Rubble reef flats are composed of materials derived from the reef front. Here, live coral is broken, accumulates in situ, and is picked up and transported up on to the rubble flat. Transport occurs as two separate but related processes: (1) the initial dump of a mixture of material on the outer flat and (2) the physical separation and sorting of that material on the rubble flat itself. The intensity and frequency of these processes are a function of wind strength, sea state, and tidal condition. Breakage, storage, transport, and dumping on the outer rubble flat and sorting on the flat itself occur at specific energy levels and therefore at specific times and tidal states. Low-energy conditions at One Tree Reef occur throughout most of the year, and in these periods, sand entrainment and transport to the lagoon and sorting of finger rubble on the rubble flat are predominant processes. Intermediate-energy conditions commonly occur during the March and June solstice and equinox cycles when the major processes/products operating are wave destruction/accumulation of branched corals on front, transportation of branched forms to form rubble flat spurs, separation of massive and plate corals on the rubble flat, and imbrication of large clasts.

High-energy conditions predominate in the same time frame, during which time major wave destruction of massive and plate corals and the accumulation of chaotic rubble occurs on the on front.

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## Cross-references

Acropora  
 Algae, Coralline  
 Algae, Turf  
 Algal Rims  
 Bioerosion  
 Boulder Zone/Ramparts  
 Bryozoa  
 Coral Reef, Definition  
 Corals: Biology, Skeletal Deposition, and Reef-Building  
 Corals: Environmental Controls on Growth  
 Foraminifera  
 Forereef/Reef Front  
 Great Barrier Reef Committee  
 Lagoons  
 Microatoll  
 Molluscs  
 Reef Flats  
 Reef Front Wave Energy  
 Scleractinia, Evolution and Taxonomy  
 Sediments, Properties  
 Shingle Ridges  
 Tidal Effects on Coral Reefs  
 Wave Set-Up  
 Wave Shoaling and Refraction  
 Waves and Wave-Driven Currents

## REEF FRONT WAVE ENERGY

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## Synonyms

Forereef; Reef Slope; Seaward Slope

## Definition

The reef front is the downward-sloping reef section, seaward of the reef crest that normally ends in a sediment apron. Waves undergo transformations over the sloping reef front that redistribute and dissipate their energy.

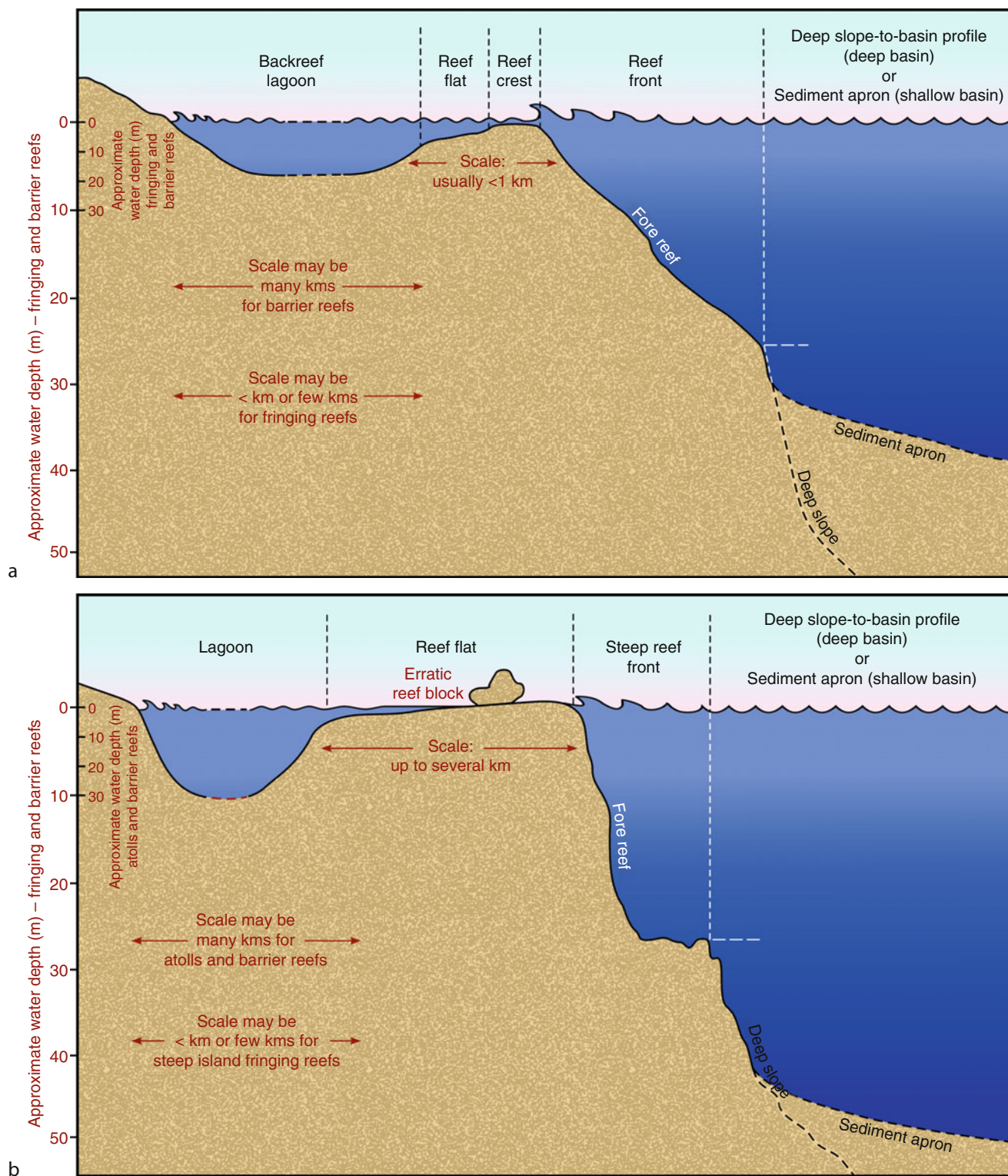
## Introduction

From the reef crest to depths of 20–25 m, [Figure 1a](#), (fore reef of [Stoddart, 1969](#); [Milliman, 1973](#)) intense sunlight, strong water motion, and nutrients support coral and coral-line algal growth in well-known forereef zones and construct an extensive reef framework. Spurs and grooves with vertical relief of ~2–20 m frequently occur in this reef front zone ([Roberts et al., 1975](#)). Forereef sediments are mainly biogenic sands or coarser particles in pockets, channels, and thin veneers ([Longman, 1981](#)). Seaward and deeper than the forereef (20–25 m), [Figure 1b](#), the lower or deep forereef slope has less sunlight, weaker flows, limited growth of reef-building organisms, and fewer reef framework organisms that include coral heads, gorgonians, and algae ([Stoddart, 1969](#)). Fine sediments in this section consist mainly of coral debris and particles of calcareous algae from shallower areas as well as reef rubble and blocks ([Longman, 1981](#)). The lower slope of the reef front is highly variable between reefs and within each reef, but generally tends to increase in steepness from fringing to barrier reefs and atolls ([Gourlay, 1996](#)). Wave–bottom interactions are affected by the steepness and morphological configuration of the seafloor in both the forereef and deep reef front slope.

Wave–reef interactions start at the lower slope and continue to the breaking point near to and generally seaward of the reef crest. Wave changes across the reef front depend on incident wave period and height and start at water depths  $\leq 50$  m (wave periods  $\geq 8$  s) for most energetic waves. These transformations drive a cross-reef current identified by Munk and Sargent ([1948](#)). Seminal work by Gerritsen ([1981](#)) applied the wave radiation stress concept to wave interactions with coral reefs and established a basic analytical approach in this field. Subsequent oceanographers unraveled other details of wave processes on coral reefs that are summarized by Monismith ([2007](#)). Waves transiting the reef front affect coral and fish zones (e.g., [Bradbury and Young, 1981](#); [Friedlander et al., 2003](#)), productivity, removal of sediments and metabolic wastes, replenishment of nutrients and distribution of food particles ([Patterson et al., 1991](#); [Hearn et al., 2001](#)), transport of sediments (e.g., [Orme, 1973](#); [Davies, 1983](#)), photosynthesis, and calcification of corals ([Dennison and Barnes, 1988](#); [Finelli et al., 2006](#)). During storms, waves cause coral mortality and morphological changes of reefs ([Harmelin-Vivien, 1994](#)). Since Darwin's *Structure and distribution of coral reefs* in 1842, it has been recognized that waves impose major forces on coral reefs systems.

## Wave transformations over the reef front

Because wave speed decreases toward the reef crest due to decreasing water depth, advancing waves change their deepwater direction until they become nearly parallel to the reef crest. This direction change, refraction, allows deepwater wave energy to reach most reefs along a given coast. However, refraction causes shadow or low wave energy zones, as in the leeward of islands



**Reef Front Wave Energy, Figure 1** Two idealized reef fronts with both shallow and deep basin profiles: (a) less steep forereef slopes are generally associated with fringing and mid-shelf barrier reefs and (b) steep forereef profiles are typical of shelf-edge reefs and atolls.



(Roberts, 1974). Spurs and grooves align with incident wave direction across the reef front in response to wave refraction (Munk and Sargent, 1948; Roberts, 1974). Wave energy propagates into the lagoons of some reefs by refraction (Lugo-Fernández et al., 1994). Refraction focuses waves along a reef resulting in wave height increases. A decrease in wave height occurs when the waves are defocused or spread. These wave height changes reflect energy redistribution, not dissipation. Waves propagating toward the crest experience a decrease in wave group speed because of decreasing water depth, and wave height increases to keep the energy density constant. This process, called shoaling, increases the wave height across the reef front without energy dissipation. When energy dissipation is small (e.g., reefs with smoother bottoms), wave shoaling and refraction dominate wave height change across the reef front up to the breaking point (Lugo-Fernández et al., 1994; Hardy and Young, 1996). In this case, the reef front wave height is estimated as

$$H = K_S K_r H_0 \quad (1)$$

where  $H_0$  is the incident wave height,  $K_s$  is the shoaling coefficient, and  $K_r$  is the refraction coefficient.

A more realistic description of wave energy across the reef front is the one-dimensional steady energy conservation equation with dissipation

$$\frac{\partial(Ec_g)}{\partial x} = -(\varepsilon_f + \varepsilon_b) \quad (2)$$

where  $E$  is the wave energy density (proportional to wave height squared),  $c_g$  is the wave group speed,  $x$  is the cross-reef distance, and  $\varepsilon_f$  represents the energy dissipation rate per unit area for bottom friction, and  $\varepsilon_b$  is a similar quantity for wave breaking. For a review of wave modeling, see Cavaleri et al. (2007). Equation 2 states that wave breaking and bottom friction dominate wave energy dissipation over coral reefs but excludes nonlinear effects and dissipation by deformable or permeable bottoms. Massel and Gourlay (2000) incorporated shoaling and refraction in Equation 2.

Because of the presence of large frame-building corals, the reef front exhibits considerable bottom roughness ranging from ~0.2 to 2 m. Bottom roughness decreases as depth increases (Nunes and Pawlak, 2008). Large bottom roughness results in higher drag or bottom frictional coefficients (e.g., Lugo-Fernández et al., 1998a) as confirmed by estimated drag/friction coefficients from Pacific and Caribbean reefs in Table 1. These coefficients are considerably larger than coefficients for sandy bottoms. The important result of higher frictional coefficients is that bottom friction is high and comparable to wave breaking dissipation and cannot be neglected when modeling (analytical or numerical) waves and currents over the reef front.

The final and most dramatic wave transformation over the reef front, visually and in terms of change to the wave form, is wave breaking. Yet, in physical terms, wave breaking is the least understood of wave transformations. While wave breaking is qualitatively well known, researchers resort to semi-theoretical approximations to incorporate wave breaking in models. Usually, waves break near the reef crest, where their height equals  $H_{\max} = h_b \gamma$  ( $h_b$  is the breaking depth and  $\gamma$  is the breaking index). In sloping reefs  $\gamma = 0.7$ – $1.0$  and  $\gamma = 0.55$  at the reef flat; functionally  $\gamma = 0.55 + 0.88 \exp(-0.012 \cot \beta)$  where  $\beta$  is the reef front slope and  $\exp$  is the exponential function (Nelson, 1994). The reef front slope also controls wave reflection. A steeper slope reflects more energy. In most instances, wave reflection appears to be small because the extreme bottom roughness appears to cause diffuse reflection. In the case of breaking waves, large amounts of energy are lost to turbulence and the wave spectrum flattens in the gravity region, but harmonics and infragravity waves may be excited by associated nonlinear processes (McGehee, 1994; Hardy and Young, 1996). Table 2, which updates Table 1 in Roberts et al. (1992), shows that wave energy changes from 72% to 99% mainly through a combination of dissipation and redistribution. In some reefs, frictional dissipation across the front reef exceeds wave breaking (Lugo-Fernández et al., 1998b; Lowe et al., 2005). Because energy dissipation (e.g.,  $\varepsilon_f$  and  $\varepsilon_b$ ) depends on water depth, this dissipation

**Reef Front Wave Energy, Table 1** Bottom friction coefficients of coral reefs

| Friction coefficient | Friction law | Method of calculation           | Reference                     |
|----------------------|--------------|---------------------------------|-------------------------------|
| 0.015–0.025          | Quadratic    | Surface slope = bottom friction | Wolanski and Pickard (1983)   |
| 0.1–0.25 m/s         | Linear       | Fitting model to observations   | Symonds et al. (1995)         |
| 0.088–0.0118         | Quadratic    | Surface slope = bottom friction | Baird (1996)                  |
| 0.06–0.02            | Quadratic    | Surface slope = bottom friction | Lugo-Fernández et al. (1998a) |
| 0.08 m/s             | Linear       | Fitting model to observations   | Lugo-Fernández et al. (2004)  |
| 0.009–0.015          | Quadratic    | Reynolds stresses               | Reidenbach et al. (2006)      |
| 0.035                | Quadratic    | Fitting model to observations   | Tamura et al. (2007)          |
| 0.015                | Quadratic    | Surface slope = bottom friction | Coronado et al. (2007)        |
| 0.28*                | Quadratic    | Bottom stress                   | Lowe et al. (2005)            |
| 0.48–1.0*            | Quadratic    | Bottom stress                   | Lugo-Fernández et al. (1998b) |
| 0.015–1.0*           | Quadratic    | Energy balance                  | Gerritsen (1981)              |

\*Dissipation factors for waves.

**Reef Front Wave Energy, Table 2** Wave energy dissipation during wave breaking on coral reefs

| Energy decay (%) | Location  | Instrumentation                | Reference                     |
|------------------|-----------|--------------------------------|-------------------------------|
| 75               | Caribbean | Pressure sensor                | Roberts et al. (1975)         |
| 97               | Caribbean | Pressure sensor                | Lugo-Fernández et al. (1994)  |
| 86               | Pacific   | Surface tracing and ultrasonic | Kono and Tsukayama (1980)     |
| 81               | Pacific   | Capacitance and photographic   | Lee and Black (1978)          |
| 81               | Pacific   | Capacitance and photographic   | Gerritsen (1981)              |
| 72               | Caribbean | Pressure sensor                | Roberts and Suhayda (1983)    |
| 95               | Pacific   | Wave hindcast                  | Munk and Sargent (1948)       |
| 78               | Caribbean | Pressure sensor                | Lugo-Fernández et al. (1998b) |
| 90               | Caribbean | Pressure sensor                | Lugo-Fernández et al. (1998c) |
| 93               | Wave Tank | Capacitance                    | Nelson and Lesleighter (1985) |
| 99               | Pacific   | Wave buoy/Pressure sensor      | Young (1989)                  |
| 80–90            | Indian    | Current meter                  | Kench (1998)                  |
| 97               | Pacific   | Pressure sensor                | Storlazzi et al. (2004)       |
| 85               | Pacific   | Capacitance                    | Gourlay (1994)                |
| 83               | Pacific   | Pressure sensor                | Lowe et al. (2005)            |
| >90              | Pacific   | Pressure sensor                | McGehee (1994)                |

is modulated by tide, ~13% in microtidal areas (Lugo-Fernández et al., 1998b,c), but higher in macrotidal settings. Two consequences of high wave energy dissipation across the reef front are: (1) reefs function as very efficient wave breakers which protect back-reef shorelines and (2) the reef front is the high wave energy zone not the reef crest which is the high turbulence zone.

### Selected effects of reef front wave energy changes

Most reef front organisms have evolved to withstand everyday wave forces, but during hurricanes wave forces are large enough to severely impact the reef (Massel and Done, 1993; Madin, 2005). Because reefs function as natural breakwaters, during hurricanes and tsunamis they offer some level of protection to coastal areas behind them (Young and Hardy, 1993; Kunkel et al., 2006) but can suffer extreme damage through removal of large blocks of up to 2,000 t deposited on the reef flats (Noormets et al., 2004). Before breaking, waves lower the sea level until just before the breaking point and beyond this point sea level rises to maintain a pressure gradient that drives water into the lagoon (Lugo-Fernández et al., 2004; Gourlay and Colleter, 2005). Finally, because of the high permeability of the reef, waves transiting the reef front drive sub-reef flows that aid both, cementation and porosity development (dissolution) that makes reefs potential reservoirs for petroleum or freshwater (Carter et al., 1989; Haberstroh and Sansone, 1999).

### Summary

In summary, waves transiting the sloping reef front experience decreasing water depths and increasingly rough bottom (high bottom friction/drag coefficients) that cause refraction, shoaling, and energy dissipation (bottom friction and wave breaking). Net wave energy reductions of 72–99% have been estimated from measured wave heights over many reefs that maintain a wave height gradient across the reef front. The resulting reef front wave

field provides energy that drives or supports biological and chemical processes of the reef ecosystem, geological and morphological processes over and in the reef, and a wave-driven flow that connects the reef front to the backreef lagoon. Efficient dissipation of wave energy by coral reefs provides some measure of protection against large hurricane waves and tsunamis to backreef lagoons and shores.

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## Cross-references

Forereef/Reef Front  
 Hydrodynamics of Coral Reef Systems  
 Reef Topographic Complexity  
 Tropical Cyclone/Hurricane  
 Tsunami  
 Wave Set-Up  
 Wave Shoaling and Refraction  
 Waves and Wave-Driven Currents

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## REEF INTERCONNECTIVITY/LARVAL DISPERSAL

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## Synonyms

Larval migration; Larval transport; Natal dispersal; Reef connectivity; Reef population connectivity; Reef population network

## Definition

*Reef interconnectivity*. The flux of larvae between reef locations, creating a network of interconnected reefs – could also refer to the flux of water mass (i.e., oceanographic connectivity), transporting sediments, particulate or dissolved organic or inorganic matter, trace metals and/or pollutants from reef to reef (sensu Paris and Cherubin, 2008).

*Reef population connectivity*. The exchange of individuals among subpopulations during any stage of their life history (sensu Paris et al., 2007) – described as the “exchange of individuals among geographically separated subpopulations that comprise a metapopulation” (sensu Cowen et al., 2007). Further, “realized connectivity” (sensu Pineda et al., 2007) requires that the individual that migrates from a source population survives within the receiving population until it reproduces (or replaces itself).

*Larval dispersal*. The spread of larvae from the spawning site to a settlement site.

*Natal dispersal*. In the broader sense of the term, dispersal is the process of moving away from the birthplace (sensu Clobert et al., 2001). For *coral reefs* and reef-related species that have a sessile or benthic adult phase, dispersal is only possible during the pelagic larval phase.

## Introduction

*Coral reefs* are naturally fragmented at all spatial scales, from the patch reef to archipelago scales. Yet, patchy habitat can be connected in many ways: by the flow

transporting material or by migration of organisms, transporting genes from the parent populations. The movement of individuals between geographically separated populations represents the dynamic interactions defined as *reef population connectivity*. This terminology comes from metapopulation theory, which states that spatially structured populations with distinct units separated by space or barriers are connected by dispersal (Levin, 1969). For those species that are mobile and migrate to spawn, populations can be kept demographically open on relatively large spatial scales by adult movement. In coral reef ecosystems where most species are benthic or sessile, the interactions between breeding populations are mostly taking place through *natal dispersal* during the pelagic larval phase (Sugden and Pennisi, 2006), which represents a unique opportunity to disperse by the currents. The spatial scale of coral reef population connectivity is thus largely determined by the dispersal of larvae, and the success of their dispersal plays a critical role in the persistence of local populations, recolonization of disturbed area, and the range limits of species distributions (Levin, 2006).

## Larval dispersal in coral reef ecosystems

The life cycle of many organisms inhabiting *coral reefs* is complex, consisting of a planktonic larval phase, followed by settlement as a benthic or sessile juvenile and adult. Although the larval phase is a short portion of the life cycle of these organisms, it is critical in assuring relatively rapid dissemination of individuals in the currents. Larvae not only have radically different physiology than their benthic forms but also have very diverse morphologies, pelagic durations (from a few hours in some soft corals to weeks and months in fish and lobsters) and swimming and feeding traits (e.g., some planulae are lecithotrophic and survive on maternal reserves; planktotrophic larvae feed on selected plankton, Llopiz and Cowen, 2009). At the end of the pelagic phase, the larva becomes competent, settles, and metamorphoses into a juvenile, supplying the benthic populations. The fate of larvae is critical in sustaining populations and defining their structure. Indeed, demographic *reef interconnectivity* depends on the relative number of larvae that (1) die of predation or of getting lost (e.g., *coral reefs* occupy a tiny fraction of the ocean's bottom, Donner, 2009), (2) are self-recruiting in the parental population, (3) migrate into distant populations, or (4) colonize new suitable habitat (Gaines and Roughgarden, 1985).

The potential of large losses during the pelagic phase are compensated by high fecundity in coral reef invertebrates and fishes (Bonhomme et Planes, 2000). Thus, balancing the benefit of *larval dispersal* (e.g., reducing reef predation and competition for food, inbreeding depression, risks of extinction, and increasing the persistence of the metapopulation), against potential detriments (e.g., increasing the risks of predation, of settling far from

parent populations, reducing local *adaptations* and selective power, and of settling in suboptimal conditions and reducing post-settlement success) is still open to debate.

### Scales of connectivity

Reef interconnectivity can occur over a continuum of time and space scales ranging from ecological to evolutionary time scales. Low dispersal rates are sufficient to shift the metapopulation distribution spatial pattern over time by a turnover of local populations going extinct and becoming reestablished elsewhere (Levins, 1969). These long-term processes of historical exchange events and species persistence result in evolutionary connectivity (Hanski, 1989). On the other hand, ecologically significant connectivity usually implies that a substantial number of individuals are exchanged each generation in order to sustain linked populations. Therefore, the scales of dispersal relevant to relatively short-term temporal processes are reduced to areas of strong larval exchange and can be approximated to the mode of a dispersal kernel (i.e., probability of successful dispersal distance). Alternatively, from the evolutionary point of view, a small number of exchanged individuals is enough to maintain genetic homogeneity between discrete populations. Therefore, larval exchange relevant to evolution occurs typically at larger spatial (i.e., the tail of the dispersal kernel) and on longer temporal scales. Because of the differences between temporal scales necessary for studies of connectivity, it is critical to formulate the questions and related hypotheses before setting up empirical measurements and/or modeling study. The high levels of percent self-recruitment reported recently have drawn attention to how small the scale of dispersal can be (Jones et al., 1999, 2005; Swearer et al., 1999).

### Description of larval dispersal and reef interconnectivity

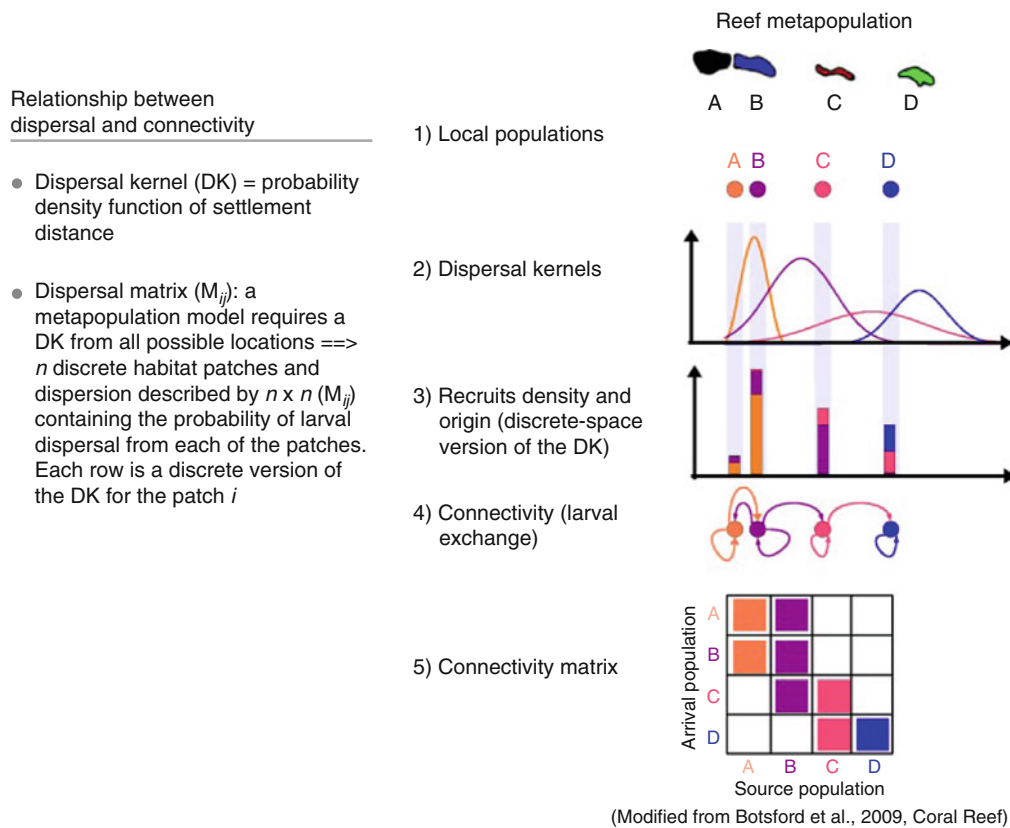
Larval transport results from the physical processes of advection and turbulent diffusion and the biological process of larval behavior. However, larval dispersion encompasses all the processes that regulate the dissemination of larvae, including spawning strategies of the parental population (i.e., reproductive mode, time, place), larval transport, survival, and settlement back to selected habitat of the coral reef ecosystem (Pineda et al., 2007). When the settlement process is not included, the terminology of “potential dispersion” is used. When the settling larvae participate to the next generation, the terms of “reproductive dispersion” or “efficient dispersion” are used.

Natal dispersal is measured by the “dispersal kernel”  $K(x,y)$ , the function that describes the probability of a larva to disperse at different distances, or the probability density function (pdf) of the number of settlers versus distance from the adult source (Nathan, 2006). The dispersal kernel is thus a continuous function that represents the

spatial distribution of larval dispersal and is typically represented in two dimensions (Siegel et al., 2003). Because the probability of mortality during larval dispersal is not null, the integral of the distribution in space is always less than 1 ( $0 \leq K \leq 1$ ). The modal distance has demographic relevance, defining population spatial patterns and persistence, while the tail represents Long Distance Dispersal (LDD) with evolutionary implications such as genetic variability and species range expansion (Paris et al., 2007). In empirical estimates, the dispersal kernel may represent a single, or at best a few spawning events from a single location (Figure 1). But to have a probabilistic power, the dispersal kernel should be calculated for a series of spawning times over multiple spawning seasons. So far, only numerical modeling can achieve this level of temporal resolution (Botsford et al., 2009).

Dispersal kernels vary with time and space, driven by spawning location and timing. Indeed, local *hydrodynamics* and larval transport are influenced over a wide range of scales by climatology, the geomorphology of the coastline, the reef topography, and fragmentation (Paris et al., 2002; Munday et al., 2009). Thus, dispersal kernels should differ among locations for species with extended reproductive season (e.g., year-round, lunar cyclic spawning in damselfish). Alternatively, they may be stable with low variance for mass spawners that disseminate their gametes over a very narrow window in time (Baums et al., 2006; Sadovy-Mitcheson et al., 2008). Because larval dispersal includes larval traits and behavior, the shape of the dispersal kernel certainly varies among species (Steneck et al., 2009) from being asymmetrical in cases of high local retention, to bimodal for areas of divergent currents or for species that have a plastic larval competency and relatively long maximum competencies (Shanks, 2009; Butler et al., in review Limn. Oceanogr.). Finally, the magnitude of the dispersal kernel varies as a function of larval mortality, its mode as a function of the advection, and its variance as a function of current variability and diffusion (Paris et al., 2007; Botsford et al., 2009).

Dispersal kernels from multiple spawning locations form the “connectivity matrix.” Each node  $i$  on the x-axis and node  $j$  on the y-axis of the square matrix represents a spawning and settlement location, respectively, while each cell  $M(i,j)$  represents the probability that a larva from a natal reef  $i$  migrates to the settlement reef  $j$  during its pelagic larval duration. Values on the matrix diagonal, when  $i = j$ , represent self-recruitment. Estimating reef interconnectivity will help determine the size of the subpopulations forming a metapopulation. Alternatively, if there is an a priori knowledge of the size of each subpopulation (e.g., based on population genetics), each node  $i$  represents the center of mass of a subpopulation located in a coral reef area  $S_i$ . Probabilities of larval linkages between the subpopulations will help map the metapopulation in which they belong. Metapopulations are thus separated by dispersal barriers.



Reef Interconnectivity/Larval Dispersal, Figure 1 Relationship between dispersal and connectivity.

### Influence of hydrodynamic and biological process

In idealized coastal models described by Siegel et al. (2003), the dispersal kernel only accounts for advection by stationary mean currents and turbulent diffusion, determined by the temporal scales of current fluctuations. While diffusion tends to increase local retention over multiple generations, advection increases the spread of the species. The relative importance of the two processes can be defined by the Peclet number ( $P_e$ ).

Recent studies indicate that despite their small size, coral reef fish larvae are not passive (Leis, 2007 for review). They have a diversity of traits and considerable behavioral capabilities that can lead to successful completion of the early pelagic life phase (Paris et al., 2007). In particular, vertical migration during ontogeny increases retention near natal reefs and decreases dispersion losses, likely enhancing survival (Paris and Cowen, 2004). Larvae can come back to their native reefs or can be exchanged among breeding subpopulations. However, the dynamics of these interactions at both the individual and population levels are not fully understood (deYoung et al., 2004). For those larvae that do not return home, the extent to which larval behavior influences their arrival pattern among adjacent and distant reefs (or larval connectivity network) is not known. More importantly, interactions of the small-scale larval movements with transport

processes due to larger-scale currents need to be quantified with regard to the spatial patterns of recruitment. Since actively moving larvae may be diluted and to some extent dispersed by currents, an in situ study of them is very difficult. Larval behavior is associated with the perceptual range of each individual, representing its informational window onto the environment. For coral reef fish larvae in particular, a suite of sensory systems operating at different scales can play an important role in orientation: acoustic (Simpson et al., 2005) and olfactory (Atema et al., 2002) signals in the shorter range, and possibly visual and magnetic signals (Kingsford et al., 2002) for longer-range navigation. Understanding the orientation behavior of larvae is a prerequisite to understanding, measuring, and predicting demographic (ecological) connectivity and may also be relevant to genetic (evolutionary) connectivity (Paris et al., 2009). Understanding how larvae orientate and the sensory cues they use for orientation constitutes one of the largest gaps in our knowledge of larval behavior.

### Reef interconnectivity and habitat

Population connectivity not only depends on life history but also on the seascape defined by both the local currents and habitat configuration. The interactions between physical and biological factors and their role in shaping



populations have been previously discussed in landscape ecology (Levins, 1969), but this discussion is a relatively recent development for marine ecosystems (Barber et al., 2002; Baums et al., 2006; Cowen et al., 2006). The spatial arrangements and connectivities of marine populations are poorly understood, yet they are assumed to enhance resilience to disturbance and be of critical importance for population persistence (Kinlan et al., 2005; Hasting and Botsford, 2006). Baums et al. (2006) demonstrated that patterns of connectivity are indeed linked to the fragmentation of the coral reef habitat. Connectedness (i.e., number of connected subpopulations) and connectivity networks are changed with extended larval competency period only when distances between habitat patches are significant. This implies that the response from reef populations to *climate change* through the growth rate and survival of the early life history stages is a nonlinear process and may be counterintuitive. Indeed, dispersal kernels are not necessarily shrinking with increased temperature (Paris et al., 2008; Munday et al., 2009).

Maintaining the reef system as pristine as possible is important since it affects the production of larvae and their settlement survival, and subsequently, their recruitment into the adult population (i.e., “realized connectivity” sensu Pineda et al., 2007) and resilience in response to disturbances. Reef damage also impacts reef interconnectivity through the loss of habitat patches that may serve as stepping stone linkages for the population network. Reefs depend on pristine areas for larval production, which is necessary for long-term persistence. If pristine areas are not maintained, eventually the entire reef will likely be lost.

*Coral reef conservation* would benefit from greater understanding of the degree of connectivity between *coral reefs*, or between land and reefs, that may exist through the movement of water masses (Paris and Cherubin, 2008). Land use, such as clearing of native vegetation and replacement with intensive agriculture, has increased pollution transport to the coastal ocean to a level many times the natural rate (McKergow et al., 2005). Degraded water quality of streams has yielded degradation of receiving bodies, such as lagoons and coastal waters, where most *coral reefs* reside. Sediments and nutrients, in excess, are almost universally recognized as having inhibitory or negative effects on reef communities.

### Estimating reef interconnectivity

Larval dispersal is described by the number of larvae  $N$  dispersed as a function of the distance  $y$  from the birth place. Another way to represent dispersion is to describe a dispersal kernel representing the probability density function (PDF) to find a larva at a distance  $y$  from its birth location. In other words, it is the probability that a larva settles at a given distance from its source population. Measures of natal dispersal (sensu Clobert et al., 2001) are typically determined by the dispersal kernel  $K(x,y)$ , defined as the probability of a larva settling at a distance  $y$ , given that

it was released at a spawning location  $x$ . Dispersal kernels are thus the spatial distributions of dispersed larvae and can be represented in two or three dimensions. The modal dispersal distance from the dispersal kernel has demographic relevance (e.g., population spatial pattern, persistence), while the tail, representing long-distance dispersal, is relevant on an evolutionary level (e.g., genetic mixing, species persistence; Hanski and Gaggiotti, 2004; Steneck et al., 2006).

Currently, the spatial scales of the dispersal of reef fish larvae are estimated using indirect and empirical techniques (Thorrold et al., 2002; Jones et al., 2005; Planes et al., 2009) or modeling approaches (Cowen et al., 2000, 2006; James et al., 2002).

### Empirical approaches

Reef interconnectivity can be empirically estimated by indirect (i.e., population genetics and paternity analysis) or by direct approaches (i.e., tagging/natural markers and larval/settlement observations). Although they differ in the characteristics of the dispersal that they can quantify, empirical methods can provide evidence of (1) *connectivity*, or the strength of the paths between subpopulations (or whether a subpopulation is a source or a sink), (2) *local retention*, or larvae returning to their natal population (sensu Paris and Cowen, 2004), and (3) *self-recruitment*, or strength of replacement paths which are closed loops, typically calculated as the proportion of settlers at a location that were spawned locally (Jones et al., 1999; Swearer et al., 1999; Almany et al., 2007). The latter is a measure of isolation of a subpopulation. If almost all populations within the metapopulation exhibit high self-recruitment, then they will also be characterized by high *local retention* and narrow dispersal kernels (Botfords et al., 2009).

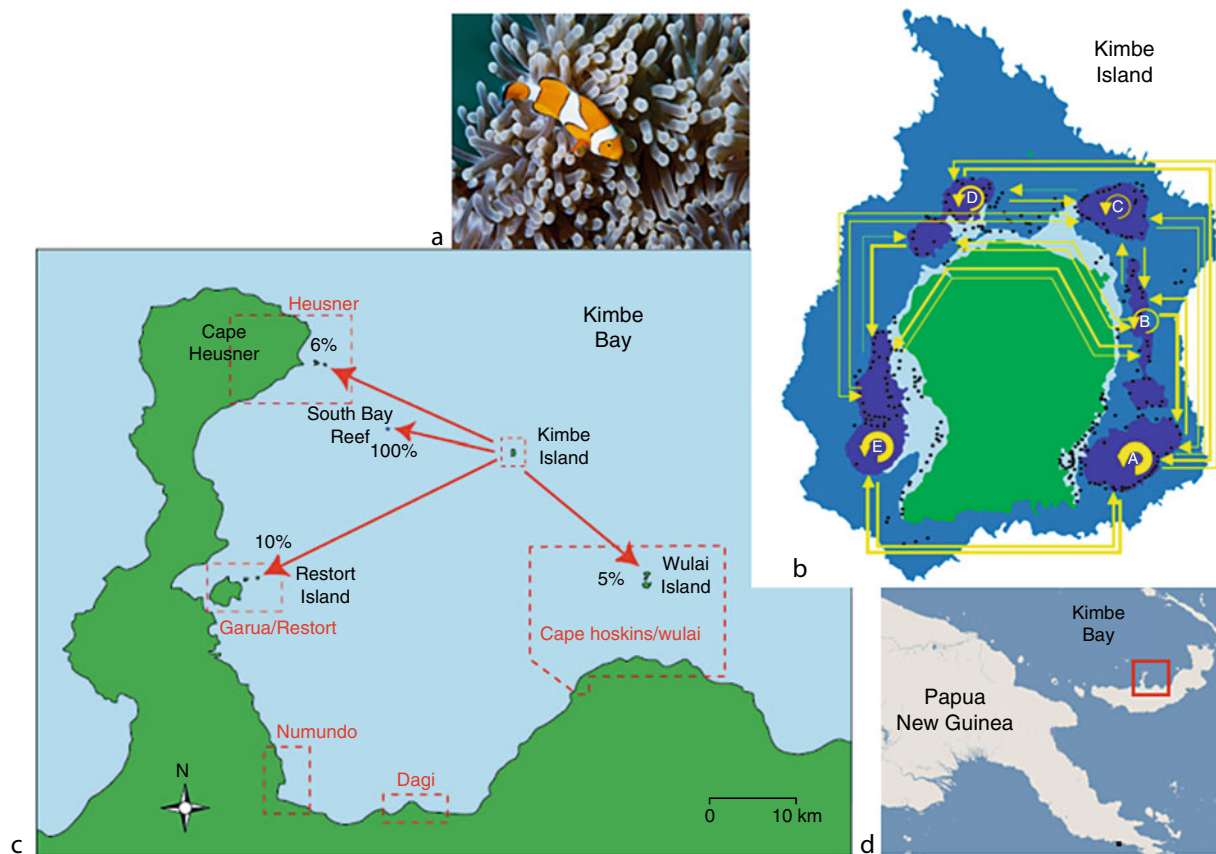
Among the indirect methods, the most commonly used is population genetics that describes *connectivity* by comparing allele frequencies among spatially discrete subpopulations. High levels of genetic similarity between populations suggests high gene flow over time. This is a valuable approach in assessing patterns and degrees of connectivity when methods to directly track larvae are not possible. Indeed, adult populations represent an accumulation of genetic signature from larval sources over time, influenced not only by larval exchange but also by ecological and evolutionary forces. Thus, such estimates of gene flow are an adequate approximation of contemporary levels of genetic connectivity only for species with relatively short life span and strictly sexual reproduction. For reef organisms with overlap across generations, population genetics may not represent present-day connectivity patterns, even for high evolving genes (Hughes et al., 2003). It is also important to note that traditional population genetic F-statistics that have been viewed as a proxy for dispersal over evolutionary time scales are not sensitive to recent changes in gene flow and genetic structure of long-lived organisms that retain the signature of past

events. Other population genetics statistics involving assignment methods can evaluate contemporary connectivity rates without the unrealistic assumptions required by traditional methods (reviewed in Manel et al., 2005). While genetic assignment techniques can link a settler to its natal reef, parentage analysis can identify its actual parent (Jones et al. (2005) provide a promising first example). Parentage analysis yields information on the critical features of dispersal for multiple spatial scales, (Figure 2). The main limitation is performing adequate sampling and collecting a significant proportion of the source adult population and new recruits over the entire potential range of dispersal (although less critical, Planes et al., 2009). Besides genetic methods, direct estimates are possible using geochemical tags recorded from the environment in calcified structures of marine larvae (i.e., otoliths, statoliths, shells). This technique can be used to determine the origin of individuals settling into juvenile habitats, or to examine natal homing of spawning adults that migrate significant distances after settlement (Becker et al., 2007; Thorrold et al., 2001). This approach provides sufficient information to estimate the larval dispersal matrix but is not appropriate to estimate dispersal kernels due to the

relatively large spatial scales of variability of water properties in coral reef environments (Thorrold et al., 1998, 2001). Finally, larval settlement tracking combined with observations of the chemical and physical environments provide accurate estimates of local retention, while allowing quantification of the role of larval behavior in shaping dispersal kernels (critical to calibrate concept-driven biophysical connectivity models). However, this approach requires extensive high-frequency sampling relevant to larval time and space scales (Paris and Cowen, 2004). In addition, local retention is difficult to measure as the reproductive output and the fate of all offspring from a particular population must be known.

### Numerical modeling approaches

Spatially explicit individual based modeling (IBM) has emerged as a key tool for understanding organism–environment interactions (Werner et al., 2001) and is particularly relevant to investigate larval fish fluxes in the complex coral reef ecosystem. Connectivity models aim at predicting the rate of exchange of individuals (i.e., larval fluxes) between the populations forming a metapopulation. Spatially explicit IBMs have become



**Reef Interconnectivity/Larval Dispersal, Figure 2** Empirical estimates of multi-scale larval linkages using DNA parentage analysis of (a) the clownfish (*Amphiprion percula*), (b) between 5 lagoons of Kimbe Is. and (c) from Kimbe Is. to marine reserves (dotted red boxes) proposed in western Kimbe Bay, (d) northeast of Papua New Guinea. Modified from Planes et al. (2009, PNAS).





the most efficient tools in connectivity studies (Werner et al., 2001). The typical output for  $n$  populations is an  $n \times n$  matrix in which element  $(i, j)$  is the probability for an individual to transit from  $i$  to  $j$ . These square matrices are called connectivity matrices or transition probability matrices, each of whose rows ( $i$ ) contain numbers summing to 1. In order to describe a system at ecological scales, the proportion of successful recruits must reflect the recruitment rates (i.e., number of recruits per generation) required to replenish the local population to a minimum of zero growth (Cowen et al., 2006). Such recruitment rates can be estimated a posteriori to match adult mortality rates using simple population growth models (e.g.,  $N_t = N_{t-1} e^{-r_t}$ ). Similarly, demographic connectivity models can be a posteriori scaled by production (e.g., relative spawning biomass per unit population or proportion of adult habitat in each population). Because connectivity models are by nature spatially explicit, it is strongly recommended to couple the Lagrangian tracking algorithm with a geographic information system (GIS). The GIS serves to delineate the source populations as well as the recruitment habitat along an individual particle's path. It is also important to incorporate the uncertainties into the connectivity model (e.g., stochastic Lagrangian model (LSM), stochastic mortality); otherwise, the analytical value of the transition matrices is limited.

The connectivity matrix describes the probability that an individual moves during its pelagic larval stage from the birthplace (or source population) to its settlement location (or sink population) as a settling larva, all in a three-dimensional dynamic system. Such transition probability matrices are of considerable value for metapopulation and genetic studies (Hedrick, 2000) as well as for spatial management and conservation issues (Urban and Keitt, 2001). We show that they also provide a method to quantify the relative influence of biological and physical factors on realized larval dispersal and on levels and spatial patterns of recruits (Paris et al., 2007).

The likelihood of larval exchange from one population to another is represented in a transition probability matrix (Paris et al., 2007). The content of a given matrix element describes the probability of an individual larva, making the transition from its source population and successfully reaching the settlement stage in the destination population. Elements along the diagonal of the matrix (where source = sink) represent self-recruitment within a population. Connections between populations may be represented by several types of matrices (Figure 3): (1) the distance matrix  $d_{ij}$  represents the distances between reefs  $i$  and  $j$ ; (2) the transition probability matrix  $P_{ij}$  represents the probability that an individual larva in node  $i$  at time  $t$  will disperse to node  $j$  at time  $t + k$ , where  $k$  is the pelagic larval duration; (3) the adjacency matrix (or edge)  $A = a_{ij}$  is a binary matrix in which each element is defined as  $a_{ij} = 1$ , if nodes  $i$  and  $j$  are connected, otherwise  $a_{ij} = 0$ . This matrix is mostly used to analyze connectivity networks (Urban and Keitt, 2001). The expected flux  $F$  from node  $i$  to node  $j$  is:  $F_{ij} = S_i / S_{\text{tot}} \times P_{ij}$ , where  $S_i$  is the size of the population

in node  $i$  and  $S_{\text{tot}}$  equals  $\sum S_i$ . We set  $S_i$  to be constant, corresponding with uniform particle release at all locations.

Models of population connectivity emphasize where and how frequently larval linkages occur, how these observed patterns are created, and output spatially explicit transition probability matrices. These connectivity matrices describe the probability that an individual moves during its pelagic larval stage from the birthplace (or source population) to its settlement location (or sink population) and are of considerable value for metapopulation and genetic studies (Hedrick, 2000), as well as for spatial management and conservation issues (Urban and Keitt, 2001). Lagrangian stochastic models (LSMs) are being increasingly applied to track the dispersal of larvae, in which motions at small scales that are not resolved by ocean general circulation models (OGCMs) are usually parameterized (Paris et al., 2005). These include motions due to small-scale currents and random or oriented motions of individual, simulated larvae (Paris et al., 2002; Siegel et al., 2003; Codling et al., 2004).

## Summary

*Coral reefs* are naturally fragmented and the complex interactions of the *reef structure* and their larval behavior with the *circulation* at a series of spatial scales (e.g., *lagoon*, *fringing reef*, and *global circulation*) determine their degree of *interconnectivity*. Typical connectivity in marine populations ranges broadly from demographic to genetic time scales depending on the strength and frequency of larval migrations (Cowen et al., 2000, 2006). However, the spectrum of *connectivity* among *corals* is still uncertain given their longevity and complex reproductive strategies. Indeed, on one hand, a few migrants could suffice to cause demographic connectivity. Conversely, migration could play only a small role on the genetic structure of corals that are highly clonal (i.e., rely mostly on asexual propagation). An integration of numerical and empirical approaches across space and timescales offers the greatest potential for advances in understanding *reef interconnectivity*, requiring more interdisciplinary interaction (Levin, 2006; Werner et al., 2008). Mapping of reef interconnectivity and identifying important coral larval pathways and corridors are keys for their *conservation* (Treml et al., 2008). Indeed, *larval connectivity* helps determine the spacing and size of *marine protected areas* (Pelc et al., 2010), prioritize the protection of critical stepping stone reefs and nodes of populations' networks, and maintain key linkages, enhancing reef resilience to *climate change*-induced stress (Mumby et al., accepted).

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## Cross-references

Adaptation  
 Climate Change and Coral Reefs  
 Conservation and Marine Protection Areas  
 Coral Reef, Definition  
 Fringing Reef Circulation  
 Global Ocean Circulation and Coral Reefs  
 Hydrodynamics of Coral Reef Systems  
 Lagoon Circulation  
 Reef Structure

## REEF RESTORATION

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## Synonyms

Addressing vessel-grounding impacts; Coral habitat restoration; Coral resource rehabilitation

## Definitions

*Resource restoration.* Resource restoration consists of an attempt to overcome, through manipulation, the factors that impede the natural recovery of an impaired resource.

*Contship Houston.* Contship is an abbreviation for container ship.

*Coral reef restoration.* Reef restoration is the process of returning damaged coral reefs to a state that is functionally equivalent to their uninjured counterparts.

*Emergency restoration.* Emergency restoration involves salvage and reattachment of at-risk coral colonies immediately following a vessel-grounding incident.

## Introduction

Reef restoration is a relatively new and rapidly expanding discipline that attempts to return degraded coral reefs to some degree of their original physical, ecological, economic, and aesthetic functionality on a much-reduced time scale, with the ultimate goal being the full, natural recovery of the impaired resource. The focus of this report is a brief summary of ship-grounding restoration practices in the Florida Keys National Marine Sanctuary (FKNMS), with emphasis on major restoration projects and lessons learned from their implementation. To include examples

of reef-restoration practices in other areas of the world is beyond the scope of this paper. For a global perspective on these and related issues, the following reports are recommended: Hatcher (1984), Salvat (1987), Guzman (1991), Clark and Edwards (1995), Harriott and Fisk (1995), Rinkevich (1995), Heeger and Soto (2000), Jaap (2000), Riegl (2001), Clark (2002), Omori and Fujiwara (2004), Challenger (2006), Kaufman (2006), Jokiel et al. (2006), Precht (2006), and Edwards and Gomez (2007).

## Legal mandate for reef restoration in the FKNMS

Section 312 of the National Marine Sanctuaries Act is a liability provision that authorizes the National Oceanic and Atmospheric Administration (NOAA) to seek damages from those responsible for injuring sanctuary resources (Davidson, 2006). The Act further mandates that NOAA “restore, replace or acquire the equivalent” of injured resources. Thus, coral reef restoration in the NOAA National Marine Sanctuaries is not a management option, but a legal requirement. Decision making for restoring injured reefs in the FKNMS is guided by findings and recommendations of the damage assessment and restoration program (DARP) and is performed by sanctuary personnel following injury assessment of the grounding site.

## Vessel-grounding injuries to coral reefs in the FKNMS

The size and nature of injuries to coral reefs from vessel groundings are influenced mainly by three factors: hull length, weight, and vessel construction material. A general rule of thumb is: the larger the vessel, the greater the injury. For purposes of assigning levels of injury, vessel-grounding incidents in this report are grouped by hull length into three categories: small (<10 m), medium (10–30 m), and large (>30 m). It is reasonable to assume that, when a 122 m (400 ft) steel-hulled cargo ship goes aground on a shallow coral reef, there will be massive destruction of reef resources. Such was the case of the M/V Wellwood that grounded on Molasses Reef, off Key Largo in the Florida Keys in August 1984 (Figure 1). Massive coral colonies were split in half, overturned, and reduced to piles of rubble (Figure 2). The area beneath the ship hull was completely scarified and flattened (Figure 3), leaving the calcium carbonate-based reef foundation (reef framework) fractured and devoid of any living corals (Hudson and Diaz, 1988).

If a large vessel remains aground for a period of days or weeks before its removal, waves and high seas can cause its hull to act like a pestle in a mortar, grinding away additional reef-framework material (Hudson and Franklin, 2005a). Prolonged shading of uninjured portions of the reef by the hull, can, after several weeks, cause shaded corals to bleach by expelling their zooxanthellae (Gittings et al., 1993). The hull of a large vessel can act as a giant plow, pushing up fragmented and intact coral colonies, coral rubble, reef framework, and sand into massive rubble berms on the periphery of the grounding site





**Reef Restoration, Figure 1** The M/V Wellwood, hard aground on Molasses Reef in the (then) Key Largo National Marine Sanctuary, August 1984. (Photo courtesy of FKNMS.)



**Reef Restoration, Figure 2** Living *Montastrea faveolata* dislodged and split in half by impact of M/V Wellwood hull. (Photo courtesy of FKNMS.)

(Schmahl et al., 2006). A large, deep-draft vessel will often strike and shear off corals and sponges and topographic highs of the reef before finally becoming hard aground. In some instances, this inbound path of destruction may stretch for hundreds of meters and may impact several thousand square meters of coral substrate (Schmahl et al., 2006). The kinds of injuries inflicted upon a coral reef when a medium-size (10–30 m in length)

vessel goes aground, while similar to many of those seen in large-vessel incidents, usually differ by an order of magnitude in size and severity.

Total reef injury sustained from intermediate-size vessel groundings rarely exceeds the 100 m<sup>2</sup> threshold. Vessels belonging to the smallest-size category (<10 m) are capable of dislodging and fracturing small coral colonies, scarifying reef framework, and generating small

volumes of rubble. Their injury footprint is usually 10 m<sup>2</sup> or less. Contact of the ship hull with structural elements of the reef is not the only mechanism for destruction in a vessel-grounding incident. Once a ship has grounded, the natural inclination of the captain of any size power vessel is to use the engine(s) to “power off” the reef to deeper water. The end result of this action is often further destruction of the reef and its underpinnings. Water forces acting upon crushed and loosely consolidated reef framework by action of the ship propeller(s) can result in the creation of prop-wash excavation features popularly



**Reef Restoration, Figure 3** Scarified and fractured reef framework at M/V Wellwood grounding site. Note crushed and flattened reef substrate in background. (Photo courtesy of Harold Hudson.)

referred to as “blowholes.” The M/V Alec Owen Maitland, a 47 m (154 ft) oil-supply vessel, grounded on a shallow reef area off Key Largo, Florida, in 1989 (Figure 4) and created a propeller-generated excavation that measured approximately 2.5 m deep by 25 m in diameter. This type of injury is inherently unstable since the crater is subject to further erosion by storm waves, as evidenced during passage of Hurricane Andrew in 1992 (Hudson et al., 2008). In addition, natural sediment infilling creates a substrate of shifting reef sand within the blowhole that is unsuitable for coral attachment. While prop-wash excavations can occur in medium-size groundings on coral reefs, they are conspicuously absent from those in the smallest vessel-size class.

Another injury feature commonly associated with vessel groundings on coral reefs is the presence of anti-fouling bottom paint within the impact area. Pressure and friction contact of the vessel hull with reef substrate often heats and peels away patches of bottom paint, embedding paint into the surface of impacted reef framework. While present to some degree on most grounding sites, dislodged bottom paint on large-vessel grounding sites is usually abundant and contaminates significant areas of reef substrate. Due to its toxic nature, this material should be removed and safely disposed off on land as soon as possible after the grounding.

#### Emergency salvage (triage) of corals in the FKNMS

After an assessment has been conducted to document and quantify the nature and extent of the grounding injury (Hudson and Goodwin, 2001), emergency salvage of dislodged coral colonies and reef-framework fragments is implemented. The surviving colonies are removed from



**Reef Restoration, Figure 4** M/V Alec Owen Maitland, hard aground in October 1989 on an unnamed bank reef south of Carysfort Reef in the (then) Key Largo National Marine Sanctuary. (Photo courtesy of FKNMS.)





**Reef Restoration, Figure 5** A grounding-dislodged and fractured colony of *Diploria* sp. Both living and dead coral elements are routinely collected and cached onsite by DARP personnel for use in rebuilding lost reef topography. Loose, on-site calcium-carbonate rock is highly prized as a material for rebuilding reef structure and, when available, is preferred over quarried limestone rocks and boulders. (Photo courtesy of FKNMS.)

loose rubble and sand and placed upright. It may be necessary to cache these at-risk corals in a suitable area near the site, or even off-site, until primary structural restoration has been completed. If the colonies are relatively small (<15 cm, or 6 in.) in diameter and in imminent danger of being lost to storm surge or high wave energy, the best emergency-salvage option may be to reattach them immediately to adjacent uninjured reef substrate. Dislodged, nonliving reef-framework fragments (Figure 5) are usually cached in sand areas adjacent to the injury site.

#### Restoration of small- to medium-size grounding sites in the FKNMS

When restoring reefs injured in small- to medium-size vessel groundings, the most effective strategy is often limited to simple reattachment of broken and dislodged live coral colonies and fragments back onto the grounding site. Epoxy cement and related epoxy-putty compounds are usually the most cost-effective adhesives when reattaching small-diameter (10 cm or less) colonies or live coral fragments (Jaap et al., 1996). Heavy-duty electrical tie wraps can also be used to reattach pieces of small (>30 cm) fragments of live branching corals to a parent colony or to a dead coral outcrop. Reattachment of coral colonies and dislodged reef framework greater than 10 cm is usually more cost-effective with Portland cement. Hudson and Diaz (1988) provide a basic formula and application instructions for a quick-setting (4–6 min) adhesive that combines Portland cement with molding plaster (Figure 6). Portland cement can also be combined 50/50% with construction-grade sand to produce



**Reef Restoration, Figure 6** A broken branch of live elkhorn coral, *Acropora palmata*, reattached to the reef with quick-setting Portland cement. Note gray mass of cement under coral at lower right. Another reattached fragment can be seen above, beneath the diver's swim fins. (Photo courtesy of Jeff Anderson.)

a cement grout that will remain workable under water for 30 min or more (Figure 7).

It is usually impossible to determine the original position, sizes, and number of dislodged reef elements on any but the smallest grounding site. By surveying unimpacted coral reef communities (control or reference areas) that are immediately adjacent to the injury site, number and size of reef outcrops, coral size, density, and species composition can be reasonably estimated. These data are routinely collected as part of grounding-injury assessment protocol and thus serve a dual purpose to aid researchers in reattachment of dislodged reef biota and recreation of topography that approximates pre-grounding conditions.

#### Restoring large-size grounding sites in the FKNMS

Whereas many of the injuries to reefs resulting from small- and medium-size vessel groundings may be





**Reef Restoration, Figure 7** Three intact specimens of knobby cactus coral, *Mycetophyllia aliciae*, one smooth brain coral, *Diploria clivosa* (touching diver's finger), and a small fragment of mountainous star coral, *Montastrea faveolata* (between largest and smallest *M. aliciae*) cemented to a fiberglass "tent" with a 5 cm (2 in.) thick layer of 50/50% Portland cement and sand grout. (See Anderson et al., 2008; photo courtesy of Jeff Anderson.)

addressed through reattachment of broken and dislodged corals, there are incidents where the destruction of reef elements is so catastrophic that natural recovery is unlikely to occur. Recent history has demonstrated that these major grounding sites on shallow coral reefs in the FKNMS will continue to degrade and, if left untreated, will worsen considerably as a result of high-energy (hurricane) impacts (Hudson and Franklin, 2005a, b; Hudson et al., 2008). Moreover, even without a disruption by hurricanes, the injured reef and habitat that it once provided would not be regenerated for decades (Gittings et al., 1993; Precht et al., 2001).

Stabilization and reconstruction of crushed and flattened reef framework are required to allow eventual natural recovery of these grounding sites. To implement a reef-repair project for an injury of this magnitude requires numerous state and federal permits and a highly detailed engineering plan. Offsite and onsite construction and the use of a barge, crane, tug, and commercial divers to place and secure reef-restoration components are also required (Figures 8–12). FKNMS (DARP) personnel provide technical oversight of these projects.

Locally quarried limestone boulders, concrete, and fiberglass-reinforcement rods are currently the primary materials of choice to fabricate and install reef-replacement structures (Hudson and Franklin, 2005a, b). For additional information on coral reef restoration and monitoring in the Florida Keys National Marine

Sanctuary, the reader is directed to the following NOAA website: <http://noaa.sanctuaries.gov>.

### Lessons learned

In terms of lessons learned, hurricanes are quite literally "a force to be reckoned with." In 1992, Hurricane Andrew caused severe collateral injury to the 1989 M/V Alec Owen Maitland grounding site (Hudson et al., 2008). Failure of critical structural-repair elements at the container ship M/V Contship Houston restoration site during passage of Hurricane Georges in 1998 focused attention on the need for adequate consideration of long-term stability of reef-restoration components (Schmahl et al., 2006). Hurricane Georges also exposed another type of structural deficiency at the Wellwood grounding site off Key Largo. In 1998, Hurricane Georges removed nearly all of the hard corals that had been transplanted at the grounding site in 1985 (Hudson and Diaz, 1988; Hudson and Franklin, 2005b). A post-hurricane survey (JHH, unpublished data) revealed that more than 90% of transplants were dislodged when hurricane-force waves and ground swells excavated 14 large craters within the main injury area.

With the exception of the M/V Contship Houston site, restoration of the above grounding sites was delayed by 5 years or more. In the interim, hurricane strikes resulted in considerable expansion of the areas of original injury. It can be reasonably assumed that the significant added destruction inflicted by these storm events resulted in increased restoration costs.



**Reef Restoration, Figure 8** One of 40 900 kg (20,000 lb), pre-cast concrete reef armor units installed at the M/V Maitland grounding site in 1995. (Photo courtesy of FKNMS.)



**Reef Restoration, Figure 9** Seaward edge of a Reef Armor Unit at the M/V Maitland site, 10 years after installation. The module surface is completely coated with a thin layer of crustose coralline algae. It is widely recognized that hard-coral planulae have a strong preference for settling on substrates that have been pre-conditioned by certain species of this lime-secreting plant. Blade fire coral, *Millepora complanata*, left of center, and a brain coral, *Diploria labyrinthiformis*, center, have recruited to the thin, hard rind of crustose algae. Note profusion of gorgonians (soft corals), primarily *Pseudopterogorgia americana*, that have colonized crevices along the base of the module. (Photo courtesy of Jeff Anderson.)

## Conclusions

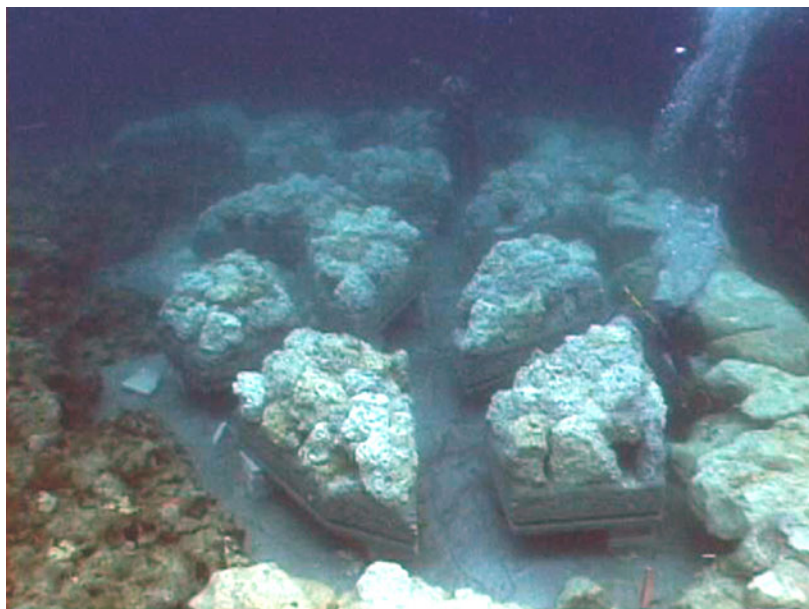
Restored vessel-grounding sites in the FKNMS are slowly recovering, as evidenced by FKNMS monitoring reports on recruitment of crustose coralline algae, soft and hard



**Reef Restoration, Figure 10** Photo shows one of 22 Reef Replacement Modules prior to installation on Molasses Reef in 2002 at the M/V Wellwood grounding site off Key Largo. The structures were designed to replicate reef topography and create habitat for cryptic biota. A reef "cave" was incorporated inside each module as a refuge for cryptic reef dwellers. FKNMS personnel fabricated all units in Key Largo using a custom mold, poured concrete, fiberglass-reinforcing rod, and locally quarried oolitic-limestone boulders. This photo shows how the boulders are embedded into the module base. (Photo courtesy of Jeff Anderson.)

corals, sponges, mollusks, crustaceans, fish, and other reef biota onto and around restoration structures. Whether these restored areas will eventually be transformed to pre-grounding conditions is time-dependent, and the answer will most likely come from the next generation of coral reef scientists.





**Reef Restoration, Figure 11** A group of Reef Replacement Modules at the M/V Wellwood grounding site inside the largest of 14 hurricane-excavated craters. A barge crane lowered the modules to the seafloor, and commercial divers guided the units into position as shown. A special low-washout concrete mixture was then delivered via pump and hose to fill the craters, locking the Reef Replacement Modules securely into the reef. Small limestone boulders (dressing stones) were quickly embedded into the fresh concrete around the modules to create additional substrate rugosity. (Photo courtesy of FKNMS.)



**Reef Restoration, Figure 12** Photo shows Reef Replacement Module #8-A at the R/V Wellwood restoration site on February 17, 2006. Eight 5 cm (2 in.) long, branch tips of staghorn coral, *Acropora cervicornis*, were transplanted on this structure on October 29, 2003. Note that crustose coralline algae, a critical pioneer biofouling component that has been shown to induce recruitment of scleractinian coral planulae, have coated the entire exposed surfaces of limestone boulders. Also highly visible is *Dictyota* sp., a seasonally abundant brown macroalgae (olive-green overgrowth in this view) that has temporarily colonized much of the structure. Compare with [Figure 10](#) and note that only the limestone boulders project above the reef substrate. (Photo courtesy of Jeff Anderson.)



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## Cross-references

Acropora  
 Climate Change and Coral Reefs  
 Climate Change: Increasing Storm Activity  
 Conservation and Marine Protection Areas  
 Engineering On Coral Reefs With Emphasis On Pacific Reefs  
 Florida Keys  
 Reef Balls  
 Reef Structure  
 Tropical Cyclone/Hurricane  
 Western Atlantic/Caribbean, Coral Reefs

## REEF STRUCTURE

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## Synonyms

Reef architecture; Reef platform structure

## Definition

Internal structural or architectural elements of a reef system or buildup.

## Introduction

Since the recognition of subsidence as a control on coral reef formation (Darwin, 1842) and the realization of the role of glacial sea-level oscillations and low stands in reef development (Daly, 1910), coral reefs have provided a focus for marine biogeological research.

One of the principal factors that appears to determine the growth and morphology of reefs is the available space (termed accommodation), which often results from the interaction of subsidence and sea-level change. Sea-level fluctuations occur through time and are important primarily because the sea surface determines the absolute accommodation for a given reef, so that a reef growing during a period of sea-level rise will be able to build upward as space is created above it. Keep-up, catch-up, and give-up responses are possible as the reef strives to keep pace with sea-level rise (Davies et al., 1985; Neumann and Macintyre, 1986). If the reef grows to the sea surface, thereby occupying all the available accommodation, it can no longer accrete vertically and may begin to build laterally, leading to different patterns of internal architecture or reef structure.

Another factor is the availability of suitable substrate for reef growth. Corals or other colonizing communities tend to become established on rocky substrate projecting above sediment-covered marine surfaces, so that reefs may return to preferentially colonize the buildups left by previous cycles of reef growth, forming complex architecture through time. Other important controls on reef growth include sea temperature (18–30°C waters of tropical/subtropical latitudes), nutrient levels, light and turbidity, wave and tidal energy, salinity and water depth (<30 m), and the destructive energy and frequency of storms.

## Reef morphology

Reefs have three main morphological elements: forereef, reef, and backreef, each with its own biota and sediment types. The forereef slopes seaward and is composed of debris or reef-building organisms; the reef is narrow-crested or a flat-topped zone where calcareous reef framework builders are active, often capped by an algal rim found commonly beneath the breaker zone; and the backreef consists of coral communities and reef debris swept landward behind the reef, including sand sheets to mud deposits in lagoonal environments. This zonation has been described for many reefs (e.g., Florida reefs: Ginsburg and Shinn, 1964; Western Atlantic reefs: Rutzler and Macintyre, 1982; Indo-Pacific reefs: Montaggioni, 2005; U.S. reefs: Reigl and Dodge, 2008; Australian reefs: Hopley et al., 2007). Coral community structure is influenced by depth and interaction between physical

disturbance (due to storms and/or wave action and currents) and recovery time, causing (with other factors) considerable variation between reef systems (e.g., Grigg, 1994). Thus, forereef slopes may have excellent coral cover (Belize barrier reef, Caribbean Sea: Rutzler and Macintyre, 1982), or be mantled by reef debris (fringing reef at Galeta Point, Panama: Macintyre and Glynn, 1976), while still others have only sparse, robust coral cover (Ningaloo fringing reef, eastern Indian Ocean: Collins et al., 2003). At Carrie Bow Cay, Belize, the profile is outer forereef with steep inner slope, sand trough, and outer coral ridge; inner forereef with spur and groove structure, narrow intertidal reef crest; and shallow backreef with massive corals, pavements, and rubble accumulations (see Rutzler and Macintyre, 1982, Figure 31).

Within the morphological zones of the reef, different coral communities are established and also interact with physical processes, so that both the communities and the sedimentary products (essentially reef framework and reef-derived detritus, termed facies) are preserved. In a wide-ranging core study of Indo-Pacific reefs (Montaggioni, 2005), seven frameworks and three detrital facies were identified on the basis of the nature and growth shapes of dominant framework builders, and on that of the texture of sediments, respectively. Framework facies in high-hydrodynamic energy settings were dominated by coralline algae and robust-branching corals. In moderate energy environments, these were replaced by domal, tabular branching, and arborescent corals, whereas sheltered areas included arborescent, foliaceous, and encrusting coral species.

Traditionally, reefs have been grouped into fringing reefs, barrier reefs, atolls and pinnacle or patch reefs, and bank-barrier reefs. Observations during the voyage of the Beagle in 1837 led Charles Darwin to formulate his theory of atoll evolution based on volcanic island subsidence, with a fringing reef ring evolving to a barrier reef as a lagoon developed behind the encircling reef, and finally, as the crest of a volcano submerged, an atoll with a central lagoon (Darwin, 1842). This atoll-forming sequence continues by progressive plate subsidence away from hot spots along seamount chains, until permanent reef drowning occurs at the “Darwin Point” (see Grigg, Figure 2 in *Hawaiian Emperor Volcanic Chain and Coral Reef History*), beyond which atolls drown and become guyots. Patch reefs also evolve as ring structures formed by leeward accretion of detritus and progradation to culminate in atolls (Fairbridge, 1950), or wave-planated banks may be colonized by peripheral reefs to form atolls (Purdy, 1974).

## Controls on reef architecture

A number of interacting controls on growth rates and growth styles of reefs have been identified (e.g., Davies and Marshall, 1980; Hopley, 1982), which together determine overall growth responses and patterns of internal structure or reef architecture, such as subsidence rates,

preexisting topography, Holocene (last 10,000 years) sea levels, biological and ecological factors, and environmental history during reef development.

Subsidence rate varies with plate tectonic setting and can be significant to negligible at Holocene timescales. Highest rates are experienced on oceanic plates, for example, as volcanic island chains progress away from mid-oceanic hot spots, influencing atoll formation as foundations subside. Similarly, subsidence is usually significant at active plate margins, whereas mid-plate and stable passive margin settings have low subsidence rates.

The amount of subsidence controls the nature and elevation of the preexisting (or antecedent) topography on which a newly established reef grows. This topography reflects the type of substrate being colonized, and its deposition/erosion history, and preferentially colonized regions (usually topographic highs) are often reflected as prominences in subsequent reef growth and architecture.

Holocene sea-level history is a fundamental process influencing reef growth, and is the latest major episode in the glacially forced sea-level changes that have affected global climate and coral reef growth for the last 800,000 years and beyond, following Milankovitch's (1941) astronomical theory. Aside from ice cores and the marine sediment isotope record, many of our global sea-level change records come from coral reef records (Davies and Hopley, 1983; Fairbanks, 1989; Hopley et al., 2007, Chapter 3; Lighty et al., 1982; Toscano and Macintyre, 2003). Following the end of the last glaciation, when sea level stood at  $-120$  m at ca. 18,000 years ago around many continental margins, there has been a general sea-level rise to reach present level, albeit with rate changes relating to pauses and meltwater pulses, and culminating (in some parts of the world, e.g., Australia) with sea level 1–2 m above present some 6,000 years ago, followed by a fall to present level. As new potential habitat has become available around the continental margins, coral reefs in settings from oceanic islands to outer shelf to the coast have grown vertically to track the rising near-surface "reef growth window" of suitable light and temperature conditions favored by corals and their photosynthetic zooxanthellae.

### Models for reef architecture

The degree to which a reef is able to successfully track sea-level rise is indicated by keep-up, catch-up, and give-up responses, with those in the latter group becoming drowned reefs or platforms. Within a single reef, a number of growth stages may be recognized, such as colonization, rapid vertical accretion, catch-up growth with the stages recorded in accumulation rates and different coral framework communities (e.g., branching vs. head coral framework). In shallow tropical reefs (Neumann and Macintyre, 1986, Figure 3), these growth patterns are Keep-up reefs: shallow, frame-building communities throughout sea-level rise (windward shelf setting-fringing to barrier reef); Catch-up reefs: initially shallow, then deeper, and finally shallowing-upward

sequence (protected shelf, backreef patch, or bank barrier); Give-up reefs: reefs founder as reef growth lags behind sea-level rise and declines/ceases, becoming drowned or relict (deep shelf setting-deep mounds).

One approach taken to describe the variation between fringing reefs was based on the nature of the antecedent surface that they are established over as well as the proportion of framework and detrital sediments within the reef structure (Hopley and Partain, 1987).

The first of three types was simple reefs that are established while sea level is still rising over rocky foreshores. Growth is primarily vertical and composed of framework; however, once the reef surface reaches sea level, as for instance during a still stand, minor outward growth may occur. Reef-flat development tends to be restricted. The second type of fringing reefs has developed over a gently sloping substrate, particularly, older Pleistocene reefs. The reefs were initiated offshore when sea level was lower. The framework units are then attached to the shoreline through interfingered terrigenous and detrital backreef infill. The final fringing reef type is developed over preexisting sedimentary deposits including fine muds. Progradation of the reef is often rapid over the preexisting structure with the reef-flat framework forming a thin veneer (generally  $<4$  m thick) over carbonate and terrestrial debris (Hopley and Partain, 1987). This scheme was further developed by Smithers et al. (2006) and Hopley et al. (2007).

Fringing reefs generally fit within one of these three morphological types, but morphology does not indicate the mode of reef evolution. The two very important factors that affect the evolution of the reef are sea-level change and tectonic stability. These two factors are interrelated as vertical tectonic movement is equivalent to a relative sea-level change at a given reef location.

Kennedy and Woodroffe (2002) described six models (A–F) of fringing reef development based on chronostratigraphic data expressed as isochrones (time lines) in thousands of years BP. These models are based on available accommodation, as follows:

Model A: Reef accretion is vertical growing in keep-up or catch-up mode.

Model B: Reef accretion is lateral having established at a level with little or no vertical accommodation.

Model C: Lateral reef accretion occurs concurrently with deposition of non-reefal mud in the forereef zone.

Model D: Episodic progradation model.

Model E: Reef accretion is initially focused offshore creating a shallow landward lagoon.

Model F: The offshore reef structure is formed by storm processes and is essentially a rubble pile. Some landward movement of this rubble pile may occur as sediment is reworked landward.

These classifications of fringing reefs have been widened for the different reef morphologies known in the Indo-Pacific domain (i.e., fringing and barrier reefs, platform reefs, and atolls: Montaggioni, 2005) to five anatomical



types of reef system based on dominant depositional process, reflected to some extent in seismic architecture.

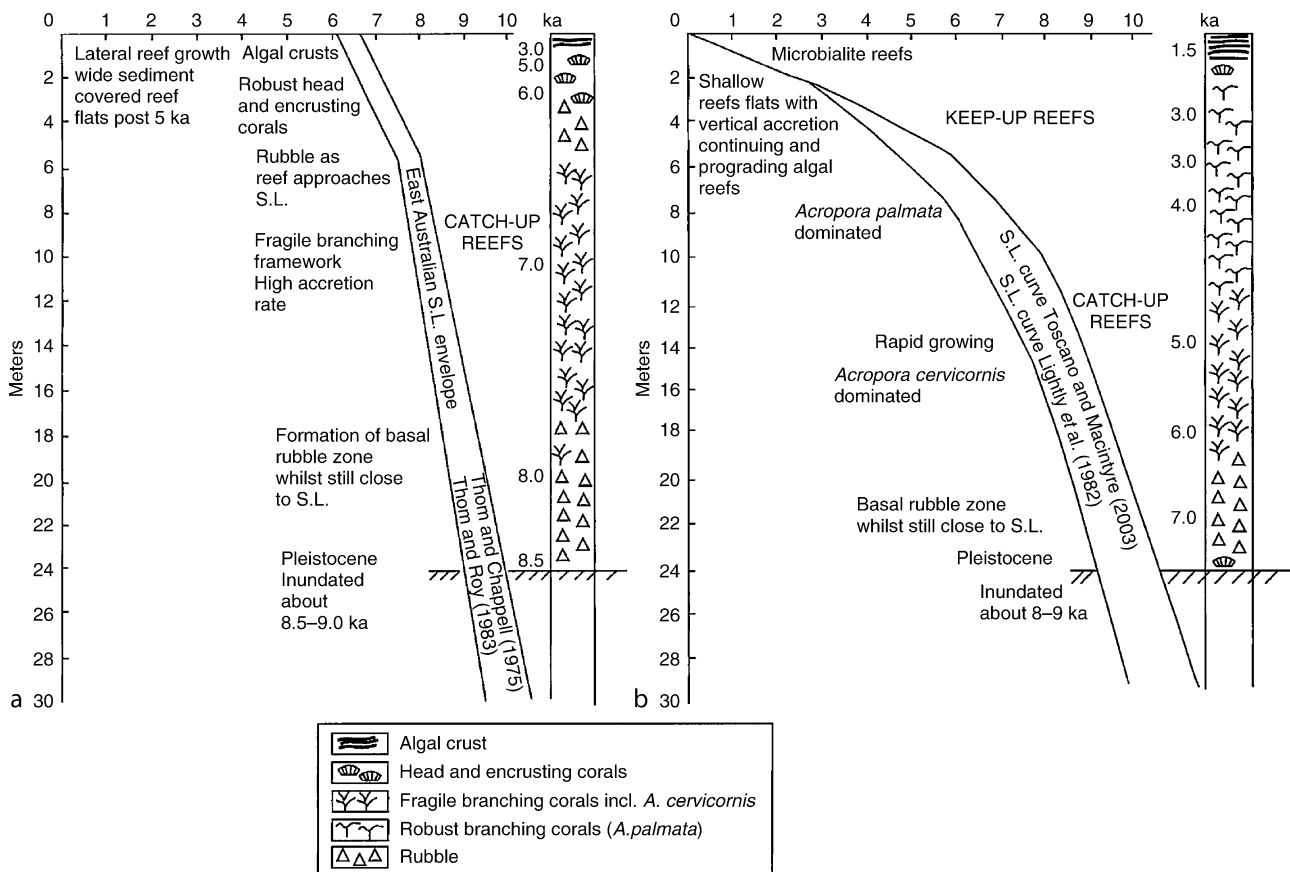
**Balanced aggrading–onlapping model:** Deposition within lagoons operated at rates close to those of the adjacent reef rim allowing the different parts of the system to reach sea level at the same time. There was a fine balance between reef rim growth through aggradation and backreef accumulation through onlapping. The dominant process refers to balanced aggradation–onlapping (Model A of Kennedy and Woodroffe, 2002).

**Seaward prograding model:** This relates to reef systems that developed seaward by lateral accretion of the forereef. They started to grow in settings where vertical accommodation was limited or missing. Such Holocene reefs mostly developed close to the shore when sea level was around its present-day position. Referring to Models B and C recognized by Kennedy and Woodroffe (2002), they are common in inner shelf sites (see Montaggioni, 2005).

**Back-stepping model:** Lateral backward accretion can occur episodically; in this case, the reef develops through coalescing of offshore patches onto the forereef zone from framework growth and/or sediment infill (Model D of Kennedy and Woodroffe, 2002; see Montaggioni, 2005).

With back-stepping reef anatomy, reef initiation occurred below modern sea level at depths where the rates of reef aggradation during the early Holocene times were not efficient enough to fill up available accommodation. The landward migration of accretion centers is assumed to result from the specific adaptation of coral communities to local environmental changes, and coral communities would be forced to displace landward to find habitat suitable for sustained growth (Engels et al., 2004).

**Unbalanced aggrading–downlapping model:** This anatomy relates to reefs that comprise a well-developed, outer rim enclosing a depressed backreef area forming through multiple depositional processes. During the earlier times of inundation, the backreef zones probably were open systems (lagoons) in which sediment accumulation was continuously disrupted by water circulation, with deposition of coral gravel. As the reef margins developed vertically, water agitation within the backreef areas decreased progressively and the sedimentation changed to sand and/or muddy sand. After the sea-level transgressive phase ended around 7,000 years BP, most of the reef rims that developed through keeping pace with sea level formed protecting barriers, thus favoring trapping of sediments



**Reef Structure, Figure 1** Contrasting sea-level curves, reef response, and reef structure for (a) Australian and (b) Caribbean reefs. (From Hopley et al. [2007, Chapter 11].)

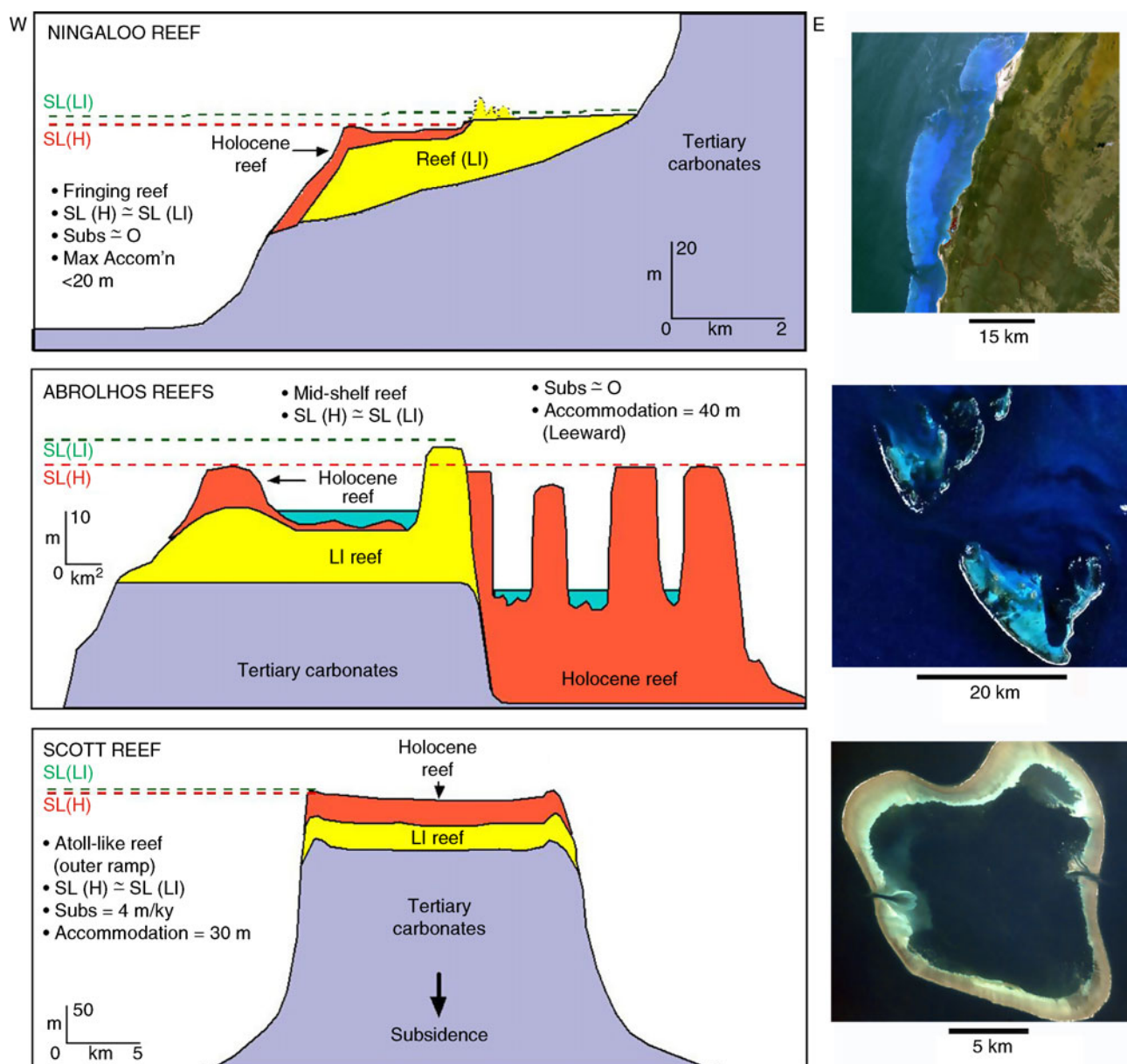
within backreef environments, and this explains why the main phase of backreef infill started at around 7,600 years BP on many reefs (see Montaggioni, 2005).

Backreef sediment sheets accumulate as downlapping clinoforms at the inflection of slope between the rim-lagoon transitional slope and lagoon floor settings.

Unbalanced aggrading-onlapping model: Backreef deposition can also occur through onlapping beds caused by termination of gently dipping to subhorizontal sheets against steeply dipping antecedent substrate or flanks of intralagoonal coral patches; the isochrons are parallel to the lagoon floor surface. Correlative to backreef infilling,

vertical accretion of the reef margins occurred until the margin top reached the present sea-level position; then, the former prograded backward over early deposited backreef sediment beds. According to their initial depth and width and the sedimentation rates, the backreef bottoms remained either under subtidal conditions, filled up completely or passed through intertidal to supratidal deposits. For examples, see Montaggioni (2005).

Differences in reef growth and structure result from contrasting patterns of postglacial sea-level rise, such as between Indo-Pacific and Caribbean reefs (Neumann and Macintyre, 1986; Toscano and Macintyre, 2003; Hopley



Reef Structure, Figure 2 Comparative architecture of Ningaloo, Houtman Abrolhos, and Scott reefs.

et al., 2007). While Caribbean reefs have steep crestral profiles reflecting vertical growth and rising sea levels in the last 6,000 years, Indo-Pacific reefs responded to slowly rising and then stable or slowly falling sea levels by lateral growth and expansion, becoming more flat topped. These contrasting patterns of reef growth are summarized in Figure 1.

### Setting, antecedent topography, subsidence and sea level change in reef architecture: a “three reefs” comparison

Three reefs with differing morphology and setting which are well known in terms of sea level history, seismic and subsurface architecture, preexisting substrate and subsidence are the Ningaloo fringing reef, the Houtman Abrolhos reefs (shelf edge reefs with atoll-like form), and Scott reef (an isolated platform with circular to arcuate reefs). The first two are in tectonically stable settings, while the third has undergone significant subsidence at Holocene timescales (Collins et al., 1993, 2003; Collins, 2009). Both tectonics and setting have influenced the elevation of the preexisting topography of the last interglacial reef (formed ca. 125,000 years ago when sea level was some 4 m above the present level along the western margin of Australia; Lambeck and Nakada, 1990) so that the pattern of Holocene reef growth and structure reflects these controls.

The Ningaloo fringing reef at latitude 20–22°S records Holocene and last interglacial phases of reef growth, but the last interglacial reef was widespread here as a fringing system whose elevation was 2–3 m above that of the Holocene transgression. Without subsidence, this coastal setting provided only limited accommodation for Holocene reef development. Consequently, the Holocene reef is relatively thin, and mantles the last interglacial reef, which provided a template for Holocene growth (Figure 2).

The outer shelf Houtman Abrolhos platforms (at 28–29.5°S) aggraded in a tectonically stable environment with the last interglacial stage of reef growth forming central platform emergent reefs, present as islands 2–5 m above sea level today. Rising Holocene sea levels partially drowned the old reef topography which was colonized in eroded portions of the last interglacial substrate, building a 10 m thick Holocene windward reef, but most Holocene reef development took place by leeward platform growth in wave-protected environments in the lee of the last interglacial platform islands, filling the entire 40 m of available accommodation and building a system of Holocene leeward reefs. The distinctive atoll-like form of the Houtman Abrolhos reefs reflects the vertical and lateral (last interglacial and Holocene) stages of reef development shown in Figure 2.

At Scott reef (at 14°S), an isolated reef, which overlies a carbonate platform, seismic profiles reveal a last interglacial reef system, but reefs, which apparently grew to sea level, are now 30 m below the present sea level,

indicating significant subsidence. Holocene reefs grew in the accommodation provided by subsidence as saucer-shaped reefs (marginal reefs with central lagoon) and are up to 35 m thick. The combination of subsidence and recurring sea-level high stands caused repeated reef stacking as a sustained pattern of reef growth (Figure 2).

### Summary

Reefs grow with distinctive morphologies such as fringing, barrier, platform, and atoll forms, preserving internal patterns of reef communities whose ecology records much of their history. They respond to important controls such as substrate, subsidence, and sea-level change, and this is reflected in their architecture. As repositories of biodiversity and records of past climates, they deserve special attention and high conservation status in our world of changing climate (see Wilkinson, 2008), increasing storms, sea-level rise, bleaching, and ocean acidification.

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## Cross-references

[Accommodation Space](#)  
[Atolls](#)  
[Back-Stepping](#)  
[Banks Island: Frasnian \(Late Devonian\) Reefs In Northwestern Arctic Canada](#)  
[Corals: Environmental Controls on Growth](#)  
[Darwin, Charles \(1809–1882\)](#)  
[Fringing Reefs](#)  
[Glacial Control Hypothesis](#)  
[Great Barrier Reef Committee](#)  
[Indian Ocean Reefs](#)  
[Subsidence Hypothesis of Reef Development](#)

## REEF TOPOGRAPHIC COMPLEXITY

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### Definitions

*Topographic complexity* is the three-dimensional arrangement of structural features over the seafloor surface, spanning all spatial scales.

*Rugosity* is an estimate of topographic complexity based on a single measurement scale.

*Roughness* is an estimate of topographic complexity based on measures spanning a range of spatial scales and pertains to the textural characteristics of a surface.

### Introduction

Coral reefs are among the most topographically complex biogenic structures in the sea. Topographic complexity (TC) exists on all spatial scales and influences a wide range of biological, chemical, and physical aspects of a coral reef system, such as water flow (Munk and Sargent, 1954; Monismith, 2007; Nunes and Pawlak, 2008) and, consequently, nutrient uptake and mass transfer rates (Shashar et al., 1996; Hearn et al., 2001), species richness and biomass (Friedlander and Parrish, 1998; Idjadi and Edmunds, 2006), and both refuge (Steele, 1999) and larval-settlement space (Idjadi and Edmunds, 2006). Because of these impacts, quantifying and mapping the spatial variability in TC is important to understanding the functioning of a coral reef ecosystem.

Two frequently used indices of TC are rugosity and roughness. Although both indices are derived from vertical-relief measurements of the reef surface, they have different computational methods, interpretive value, and limitations. The resolution of the requisite topographic data depends on the scientific question of interest. For example, studying the effects of TC on the boundary-layer flow over a single coral head would require fine-scale ( $\leq 1$  cm) horizontal and vertical topographic measurements. However, the effects of TC on reef-fish community structure could be ascertained using coarser measurements (meters horizontally and centimeters vertically), but with a larger spatial extent. Regardless of the measurement scale, the same respective algorithms apply for estimating either rugosity or roughness.

### Reef Surface Rugosity

Rugosity is most often derived from vertical profiles of surface relief, measured by placing either a chain or a profiling gauge in contact with a surface, following protrusions and crevices (McCormick, 1994; Frost et al., 2005). The ratio of the overall chain length to the straight horizontal distance between the ends of the chain on the reef is the “rugosity index,” which ranges from 1 for a horizontal line to  $\infty$  with increasing vertical relief.

The limitations of this technique are well documented (e.g., McCormick, 1994; Commuto and Rusignuolo, 2000; Pittman et al., 2009) and include the absence of an upper limit, a measurement-scale bias (chain-link size or pin-spacing in the gauge), and an orientation bias for nonisotropic surfaces (i.e., surfaces for which the vertical profile changes with the direction of the transect, such as along versus across the reef crest). The rugosity concept has been extended to two dimensions by dividing the surface area of a given region by its bounding horizontal area (Dahl, 1973; Brock et al., 2006). The result is a dimensionless index, also ranging from 1 to  $\infty$ , which indicates the increase in surface area relative to the underlying horizontal plane. While free of orientation bias, this approach shares the other shortcomings of profile rugosity.

Regardless of the approach taken, profile or area, the lack of an upper bound and a clear frame of reference makes physical interpretation and cross-study comparisons tenuous at best. Interpreting rugosity values is further hampered by the lack of a standardized measurement protocol. Both sample size (i.e., chain length or region size) and sample resolution (i.e., chain link size, pin spacing, etc.) significantly affect the resultant rugosity index. Additionally, if measurements are made over a nonisotropic surface, then the rugosity index will be biased by the orientation of the chain or profiling gauge on that surface. Finally, there is little discriminatory power to the rugosity index because it is an aggregate quantity. One cannot distinguish between a single, large vertical excursion and multiple, smaller ones with an equivalent composite contour length or surface area. Collectively, these shortcomings diminish the effectiveness of rugosity as a descriptor of TC.

### Reef Surface Roughness

Roughness is typically derived from digital elevation models (DEMs), constructed from topographic data over a given area. Acquiring such data in situ on submeter scales is hindered by the lack of suitable tools. Work at this fine scale tends to be performed in the laboratory, where topography can be measured using a two-dimensional profiling gauge, consisting of an array of equally spaced, moveable pins (Carleton and Sammarco, 1987) or an X-ray computed tomography technique (Kaandorp et al., 2005). For larger areas, possibly covering tens of square kilometers, data collection can be performed using either light detection and ranging (lidar) (Brock et al., 2004) or multibeam sonar systems (Piniak et al., 2006).

Although various spatial statistics could be used to estimate roughness, fractals represent a particularly robust approach, providing both a firm geometric framework and assessing the extent of surface irregularity over a range of measurement scales. In classical Euclidean geometry, a plane has a dimension of 2 and a solid has a dimension of 3. These objects are perfectly smooth and have zero roughness. Fractal surfaces, however, lie between these extremes and have noninteger dimensions.

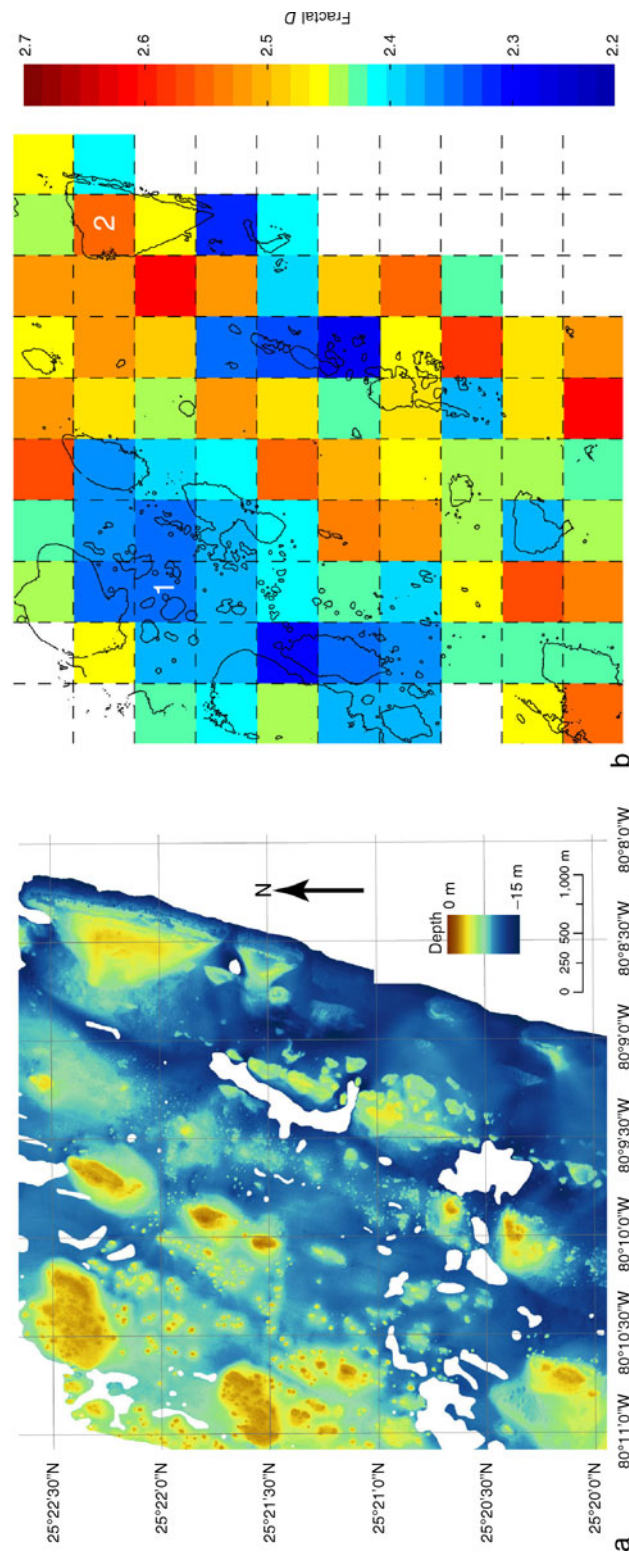
Fractals exhibit power-law scaling, meaning that spatial variations observed at one scale are replicated or are at least statistically similar to those at another scale (Mandelbrot, 1977). Fractal theory provides the basis for quantifying such multiscale variability or roughness, which is expressed in terms of the fractal dimension,  $D$ . Mandelbrot (1977) provides an overview of fractal geometry and its relevance to natural objects.

Although the fractal approach is more powerful and descriptive than the rugosity index, these benefits impose costs in terms of data requirements, algorithm complexity, and computing resources. Topographic data must span at least two orders of magnitude to validate power-law scaling. Algorithm selection is critical, because some procedures suffer from mathematical instability (Zhou and Lam, 2005). Finally, programming skill is required to effectively implement the chosen algorithm, both in terms of computational efficiency and data management.

Zawada and Brock (2009) provide an example of mapping reefscape roughness with a fractal technique. Using a DEM with 1 m spatial resolution that was derived from lidar bathymetric measurements, those authors investigated the zonation in roughness over a 5 km  $\times$  5 km portion of the reefscape in Biscayne National Park, Florida, USA (Figure 1a). That area contains carbonate sand, seagrass meadows, and a variety of reefal habitats. The study site was divided into 500 m  $\times$  500 m tiles, and the surface roughness was computed as the fractal dimension,  $D$ , for each tile (Figure 1b). The zonation patterns based on  $D$  correspond well with the geomorphic domains of each reef type at this site. Mature, large, shallow, flat-topped patch reefs (region labeled “1” in Figure 1b) have less roughness than the deeper knoll-shaped patch reefs (diagonal band of orange tiles in Figure 1b) or the crest of Pacific Reef (labeled “2” in Figure 1b), which mainly consists of encrusted, dead colonies of Holocene *Acropora palmata* and rubble. To provide a visual cue for the relation between reefscape roughness and the corresponding fractal characteristics, two regions (labeled “1” and “2” in Figure 1b) are presented both in plan view and in a three-dimensional perspective view (Figure 2a–d). Region “1” lies within the shallow patch-reef zone, and Region “2” covers the crest of Pacific Reef. The textural differences corresponding to increasing fractal dimension are most apparent in the perspective views (Figure 2b and d). Large, comparatively smooth patch reefs with high relief give way to smaller, lower relief, more numerous and jagged benthic features with increasing  $D$ . Visually, benthic substrates with larger fractal dimensions look rougher.

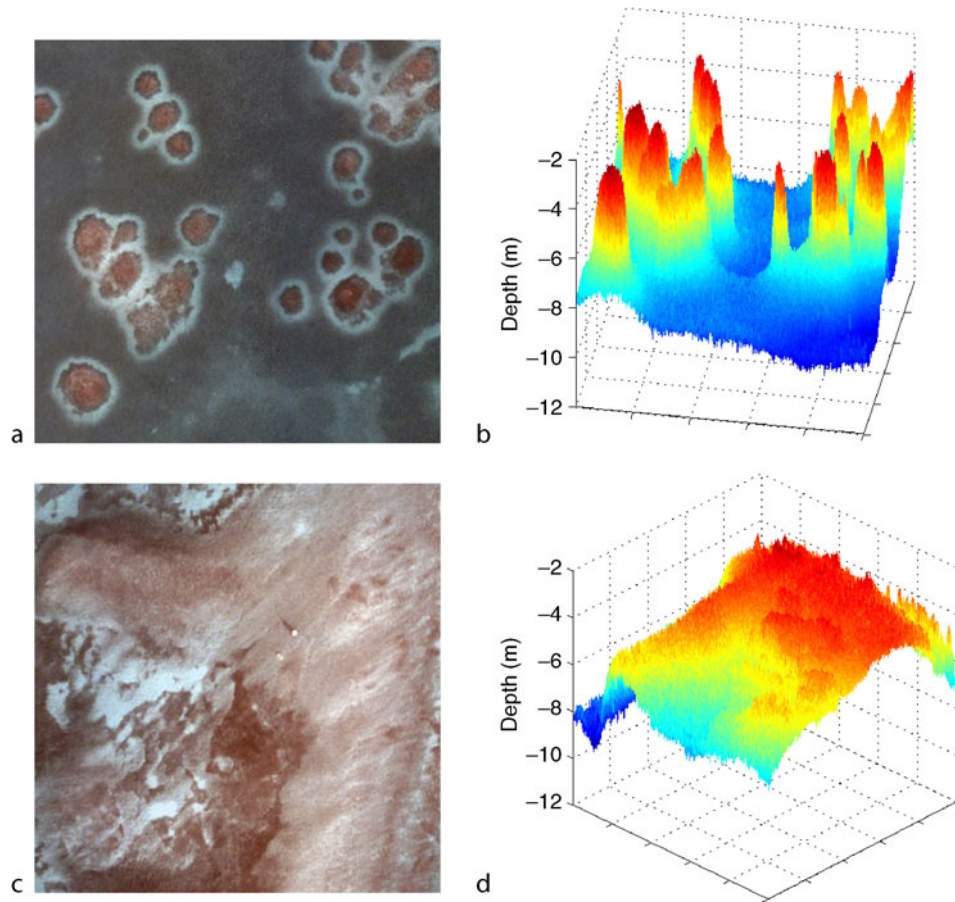
### Summary

Topographic complexity is a fundamental structural property of coral reefs that exists on all scales and affects a multitude of processes. Rugosity and roughness are the two most commonly used measures of TC. Being based on measurements across the reef surface, both indices



**Reef Topographic Complexity, Figure 1** Study site submerged topographic and roughness maps (adapted from Zawada and Brock, 2009). (a) This 5 km × 5 km area in the southern portion of Biscayne National Park, Florida, was chosen because of its mixture of reef types and the availability of a high-resolution DEM. (b) The study site was divided into 500 m × 500 m tiles. Roughness, expressed in terms of fractal dimension, was computed for each tile. For reference, the 7-m contour is plotted on top of the roughness map. The tiles labeled "1" and "2" indicate the two regions depicted in Figure 2.





**Reef Topographic Complexity, Figure 2** Detailed view of two 500 m  $\times$  500 m tiles (adapted from Zawada and Brock, 2009). The tiles indicated in Figure 1 are depicted both in plan and perspective views to convey a visual sense of roughness corresponding to their respective fractal dimensions. Panels a and b correspond to Tile 1, which lies in the shallow patch-reef zone. Panels c and d correspond to Tile 2, which is situated on the crest of Pacific Reef.

necessarily underestimate TC. Contributions from the undersides of corals and ledges are ignored, as are the insides of caverns within the reef. Rugosity is expedient with respect to data collection and processing. However, it possesses significant mathematical and implementation deficiencies, which impede interpretation beyond generalized statements of “more or less rugose” within a specific study. Although more computationally arduous, roughness overcomes these limitations and represents a holistic metric for TC.

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## Cross-references

[Antecedent Platforms](#)  
[Ecomorphology](#)  
[Florida Keys](#)  
[Geomorphic Zonation](#)  
[Patch Reefs: Lidar Morphometric Analysis](#)  
[Sediment Dynamics](#)  
[Waves and Wave-Driven Currents](#)

## REEF TYPOLOGY

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### Definition

Typology is the study of types. It is related to the classification of objects in categories according to a series of characteristics relevant for a given purpose, and the methods to achieve it. Reef typology is thus about the definition of categories of reef objects useful to study a particular aspect of coral reef processes.

### A variety of reef-related typology

Definition of a reef typology implies the selection of a number of criteria. Scales, in time and space, are key

criteria to define a typology useful to study the processes of interest (Hatcher et al., 1987; Hatcher, 1997). Reef typologies can be built for the different scales, entities, and components of the reefs, and across different scales as well.

For instance, at the finest level, taxonomy of species will look at the categories of the different living organisms based on evolutionary criteria (e.g., Veron, 1995 for corals). But in another context, organisms may be classified based on functional properties such as their metabolism. Functional typology will consider, for instance, if organisms calcify or not, if they are autotrophs or not, if they harbor symbionts or not, or where they fit in a trophic chain.

At another level of organization, coral reef habitats can be categorized using information on benthic cover (Mumby and Harborne, 1999; Diaz et al., 2000; Andréfouët et al., 2003), three-dimensional architecture, rugosity, and depth (Purkis et al., 2007). Productivity can also be an interesting criterion to classify reef zones and habitats (Smith, 1978; Kinsey, 1985). Hydrodynamics and residence time of waters have also been used to classify atoll lagoons (Andréfouët et al., 2001a).

At reef-scale, coral reefs can be described according to the diversity of habitats found on the reefs. Another common typological criterion is geomorphology, which accounts for reef shapes, exposures to hydrodynamics, position relative to nearby land masses, and depth (Stoddart, 1965; Hopley, 1982; Andréfouët et al., 2001b).

As an example of multi-scale entity, it is now common practice to define reef habitats hierarchically, by taking into account information on geomorphology, benthic cover, architecture, depth, and taxonomy of the structuring communities (corals, algae, seagrass). However, not all attributes of such a typology are easily available at all locations. Habitats can be resolved at local and global scale using geomorphological criteria and remote sensing observations (Diaz et al., 2000; Andréfouët et al., 2006), but other criteria require in situ sampling and observations to be accurate.

Obviously, the classifications criteria above are selected for particular thematic purposes. For instance, habitats can be defined and mapped to optimize conservation planning and fishery management at ecological scales (Dalleau et al., 2010; Wabnitz et al., 2010). Geomorphology can be categorized to reflect reef genetic processes at geological scales (Stoddart, 1978; Hopley, 1982; Kennedy and Woodroffe, 2002). Typology of sediment deposits provide information on local catastrophic hydrodynamic processes (Scoffin, 1993). There is virtually an unlimited number of comparative applications for which typologies can be built.

### Geomorphological typology

#### Criteria for a reef typology

In his “Descriptive reef terminology” paper, Stoddart (1978) clearly explains the difficulties in building a useful typology. He focused on geometrical and geological

aspects, but the message is valid for other descriptive and functional levels as well.

Part of the reasons explaining the difficulties in achieving one single typology accepted by all is that most existing typologies are “*derived from imperfect and perhaps biased knowledge of the range and complexity of reef phenomena.*” In other words, historical typologies have been designed using limited numbers of configurations worldwide. They were valid in one context but could not fit easily into another if they were not exhaustive.

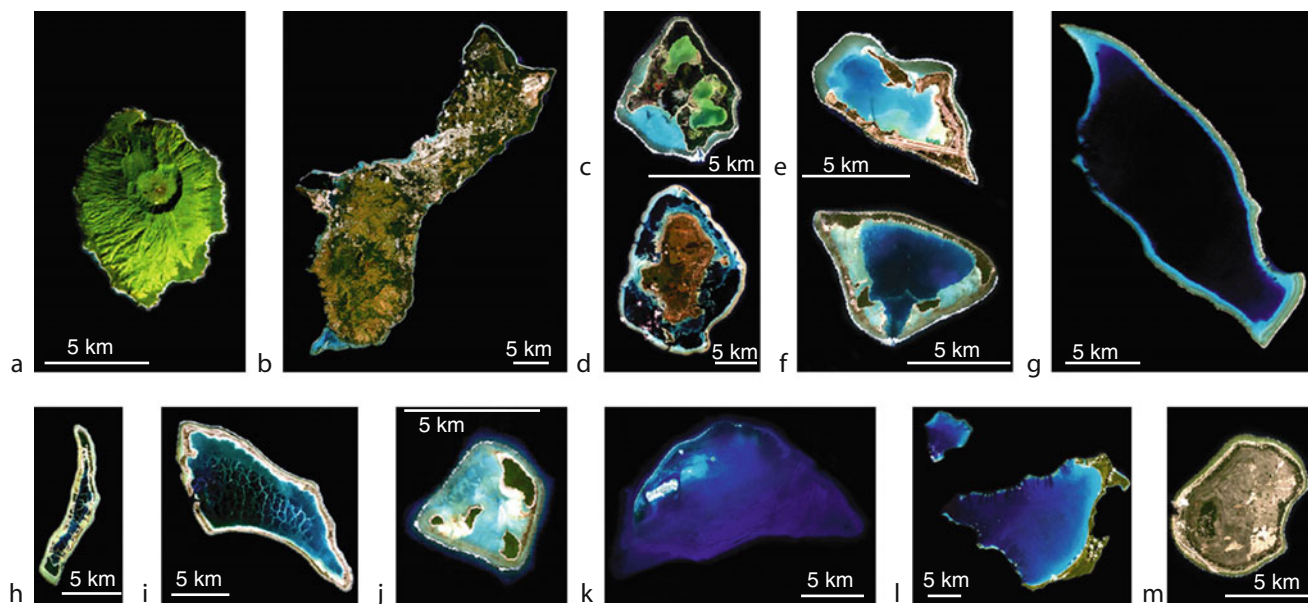
Another major issue is that geomorphological classifications have tried to merge two different criteria which are “morphology” and “genesis.” The best example is for the word “Atoll.” Initially an administrative term (*atolu*) in Maldivian language, it was assimilated by first visiting westerners as a generic term to describe annular reef (which are really *faros* in Maldivian). But it was eventually associated with the Darwin (1842) view of the fringing-barrier-atoll genetic sequence that is valid for several Pacific Ocean atolls. Thus, confusion arose on the meaning of the term “Atoll” and how to use it for new areas, as it could characterize shapes and genesis. Shape is easy to characterize, but genesis is not. The paradox is that “Atoll,” considering its theoretical Darwinian meaning,

could not be applied anymore to Maldivian atolls. Another example is the Belizean Lighthouse Atoll, which is structurally similar to the Mexican Chinchoro Bank. Yet, one is named as an “Atoll,” the other as a “Bank.”

To be useful and avoid as much as possible these problems, the terms, classes and labels of a geomorphological typology should be explicit, singular, internally correct, not redundant, innocuous, avoid radical redefinition, and be comparable among different languages (Stoddart, 1978).

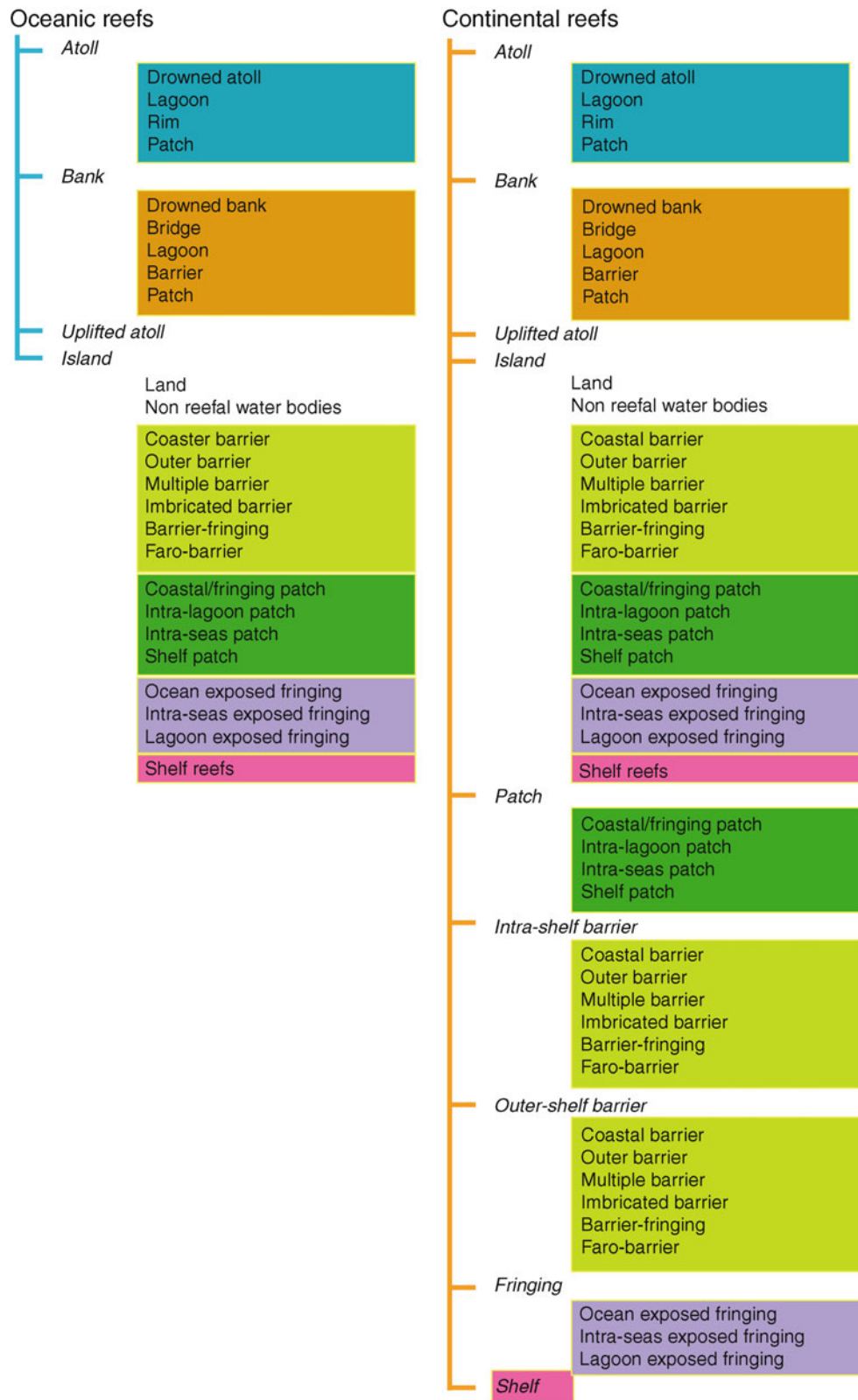
### Examples of existing reef typology

The criteria identified above are only partly met by existing typologies and definitions. Among the most structured typology, we can cite the work of Battistini et al. (1975), inspired by Madagascar, Mayotte, New Caledonia, and French Polynesia reefs. Names are provided in French, English, and German. It distinguishes at the top level 14 main classes of formations: fringing reef, boat channel, barrier reef, double or multiple barrier reef, sand cay reef, coral bank, coral head, atoll, almost atoll, faros, emerged reef, drowned reef, lagoon, and coral reef complex. Then, down the hierarchy, it is very detailed regarding fine scale geomorphological features, with



**Reef Typology, Figure 1** Examples of the diversity of Pacific Ocean atoll and island types viewed by Landsat 7 satellite. (a) Agrihan, an island without fringing reef (Northern Marianas Islands); (b) Guam, an island with fringing reef; (c) Maiao, an island with widening fringing reefs and shallow lagoons (French Polynesia); (d) Wallis Island, an island with a deep lagoon and a barrier reef (Wallis and Futuna, France); (e) Wake Island, a shallow lagoon atoll (United States); (f) Haraiki atoll, a deep atoll lagoon with a wide pass and reef islands (French Polynesia); (g) Osprey Reef, a deep atoll without islands, and narrow reef flats (Coral Sea, Australia); (h) Caroline, an atoll with shallow small reticulated basins (Line Island, Kiribati); (i) Kanton, an atoll with deep lagoon and reticulated reefs and rim islands (Phoenix Island, Kiribati); (j) Maria Ouest, a shallow lagoon atoll with islands (French Polynesia); (k) Johnston Atoll, an almost-drowned bank (United States); (l) Ouvea Atoll (right side), a raised atoll with deep lagoon (New Caledonia); (m) Nauru, a raised atoll without lagoon.





**Reef Typology, Figure 2** Main nodes of the Millennium geomorphological typology. The figure shows the three first levels, but two other levels going into greater details of descriptions exist.

14 fore reef (outer slopes) classes, 66 reef flat classes, and 19 lagoonal classes. It exemplified a key aspect of any useful typology. It is hierarchical.

In Battistini et al. (1975), typology and morphologies, and not genesis, are favored to define the broad reef types. Thus, it does not indicate any genetic relationships and processes between structures and can be considered as purely descriptive. Conversely, the fringing reef typology proposed by Kennedy and Woodroffe (2002) is based on the differences of formation of fringing structures. It is based on the internal structure of the reef, and thus can be difficult to diagnose without coring or seismic data. It is based on a limited number of examples.

Based on a larger number of reefs studied with aerial and satellite images, the Great Barrier Reef shelf reef typology proposed by Hopley (1983) is based on the description of the different units that make a reef and its lagoon (coral, rubble, algal pavement, sanded reef flat, detrital slopes and lagoon infill, shingle ramparts, aligned corals, cay, coral pinnacles, submerged reef or lagoon, and Pre-Holocene reefal limestone). The different reef types are linked by possible genetic processes. The diversity of forms and patterns reveal an evolutionary scheme relating one type to another, in terms of growth potential relative to sea level and size of antecedent platform for instance. The classification has thus two criteria: diameter of antecedent platform, and position relative to present sea level (and thus main direction of growth, lateral or vertical).

Another interesting typology made to account for genetic and dynamic processes is the typology of island-atoll proposed by Scott and Rotondo (1983). This study addressed another scale of evolution patterns compared to Hopley (1982) or Kennedy and Woodroffe (2002), since the objects of interest are entire atolls and islands (as raised atolls) of the Pacific Ocean. Scott and Rotondo's (1983) typology extends the Wiens (1962) descriptions with 11 types: volcanic island without reef, volcanic island with fringing reef, raised volcanic island with fringing reef, almost-atoll, raised almost-atoll, atoll, inundated atoll, part raised atoll with open lagoon, part raised atoll with enclosed lagoon, raised atoll with dried out lagoon, and raised atoll with typical form lost. Lithospheric processes (volcanic activity, plate movements, cooling, reheating, and compression) explain the different types of formations found in the Pacific (Allain et al., 2008). Although new information on Pacific bathymetry, seamount locations, and tectonic processes has come to light, the model describes the complexity of physical processes that can alter the different reef and island/atoll forms to provide the variety that we observe for instance in remote sensing images (Figure 1).

Hopley (1982) used aerial photographs and ERTS spaceborne imagery to refine his typology of Great Barrier Reef shelf reefs. Similar tools have been recently used to propose a hierarchical geomorphological typology for all reefs worldwide (Andréfouët et al., 2006). This "Millennium" typology (as coming from the Millennium Coral Reef Mapping Project) is a 5-level hierarchical typology

that provides a total of 800 classes that can be mapped using Landsat 30 m resolution satellite images. This high number reflects the diversity of configurations encountered worldwide and not the diversity found on any particular reef. For a given reef, between one (for a simple apron fringing reef) and 25 classes (for a complex Maldivian atoll) are frequently encountered. The main nodes of the typology are provided in Figure 2. It was designed with Stoddart's (1978) principles in mind, and tried to reconcile several local typologies while taking advantage of a global coverage of Landsat images. The typology and the maps were designed to be helpful for a wide diversity of applications including geology, fisheries, conservation, hydrology, and climate control of reef growth (Andréfouët et al., 2006). A number of coral reef atlases have been produced with this typology (e.g., for all the French overseas reefs in the Atlantic–Caribbean Ocean, Indian Ocean, and Pacific Ocean, see Andréfouët et al., 2008).

### Future typologies

The Millennium typology is the first detailed typology that was built according to the full *range and complexity of reef phenomena* (Stoddart, 1978), at least those that result in patterns visible on Landsat images. It remains descriptive, based on reef configurations and forms, although there is now evidence that the mapped products can be related to reef genesis (Andréfouët et al., 2009). Improvements will come by the validation of the map products and their interpretation using geological data.

Geology is only one aspect of reef processes. Other critical ecological and biological functions are controlled by hydrodynamics and reef complex geometrical spatial properties (e.g., reef fragmentation and larval dispersal). Therefore, it is expected that new regional typologies will be developed to account for reef geomorphology, reef geometrical properties (topology), and hydrodynamics.

Since the year 2000, old and new concepts for building habitats and ecosystem classifications have been revisited in order to help the difficult task of large-scale management of marine ecosystems (Costello, 2009). Biodiversity conservation will certainly be the main driver in establishing relevant typologies in the future.

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## Cross-references

### Antecedent Platforms

#### Atolls

Banks Island: Frasnian (Late Devonian) Reefs In Northwestern Arctic Canada

Barrier Reef (Ribbon Reef)

Boat Channel

Darwin, Charles (1809–1882)

Eastern Indian Ocean – Northern Sector

Eastern Tropical Pacific Coral Reefs

Ecomorphology

Emerged Reefs

Forereef/Reef Front

Fringing Reefs

General Evolution of Carbonate Reefs

Geomorphic Zonation

Great Barrier Reef Committee

Indian Ocean Reefs

Indonesian Reefs

Lagoons

Last Glacial Lowstand and Shelf Exposure

Last Interglacial and Reef Development

New Caledonia

Pacific Coral Reefs: An Introduction

Patch Reefs: Lidar Morphometric Analysis

Porosity Variability In Limestone Sequences

Red Sea And Gulf Of Aqaba

Reef Classification by Fairbridge (1950)

Reef Classification by Hopley (1982)

Reef Classification by Maxwell (1968)

Reef Classification, Response to Sea Level Rise

Reef Flats

Reef Interconnectivity/Larval Dispersal

Remote Sensing

Residence Time

Scleractinia, Evolution and Taxonomy

Sea Level Change and Its Effect on Reef Growth

Stoddart, David Ross (1937–)

Submerged Reefs

Western Atlantic/Caribbean, Coral Reefs

Western Indian Ocean



## REEFAL MICROBIAL CRUSTS

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### Introduction

Fine-grained, non-skeletal crusts, variously described as laminar micrite crusts, cements, stromatolites, and microbialites, are locally common in late Quaternary coral reefs. They occur on wave-swept margins in dark or low-light habitats, such as cavities and deep fore-reef slope surfaces. They have often been regarded as cements, but are now widely interpreted as microbial carbonates produced by heterotrophic bacterial communities. The crusts typically form at the end of active reef development, as late stage veneers on framework skeletons. They can be up to 20 cm thick, and locally constitute 80% of the reef structure. Crusts are particularly important in strengthening cavernous reef frameworks. Their development in poorly illuminated cavity and deepwater habitats suggests eukaryote competition for substrates. Their preferential development at wave-swept reef margins probably indicates the effect of increased carbonate saturation state by intense seawater flushing. Reefal microbial crusts appear to be more common in Late Pleistocene and Early Holocene reefs than in those of the past 6,000 years. Similar crusts are also present in much older reefs. Many questions remain concerning the factors that have controlled their formation and uneven distributions in space and time.

### Recognition

In important papers, Ian Macintyre (e.g., Macintyre, 1977, 1984) drew attention to fine-grained crusts in Holocene Caribbean reefs and reef caves. Their non-skeletal fabrics are evidently precipitated, and these examples, together with others in the Great Barrier Reef (Marshall and Davies, 1981), attracted attention as examples of submarine lithification. Outcrops of Late Miocene reefs in the western Mediterranean revealed their variable distribution and local importance. In *Porites* reefs of Messinian (~6 Myr) age in southern Spain, crust volume can far exceed that of coral. Their clotted-peloidal fabrics can be interpreted as calcified bacterial organic matter, and grains trapped in the crusts on steep or overhanging surfaces suggest adhesive biofilm (Riding et al., 1991). Following recognition of similar features in crusts in cores through late Quaternary reefs at Tahiti (Montaggioni and Camoin, 1993) and in reef caves at St Croix (Zankl, 1993), recognition and interpretation of the crusts as microbial stromatolites and thrombolites became common. They have been particularly well described by Gilbert Camoin and colleagues at Tahiti, where they were among the targets of IODP Expedition 310 in 2005 (Camoin et al., 2007).

### Structure and fabric

Reefal microbial crusts range from millimeters to decimeters in thickness (Figure 1). Their external surfaces can be irregular, smoothly domical, or patterned by 'knobby' dendritic columns (Figure 2). Internally, smooth domes are usually relatively well layered (stromatolitic), whereas the columns are usually more weakly layered.

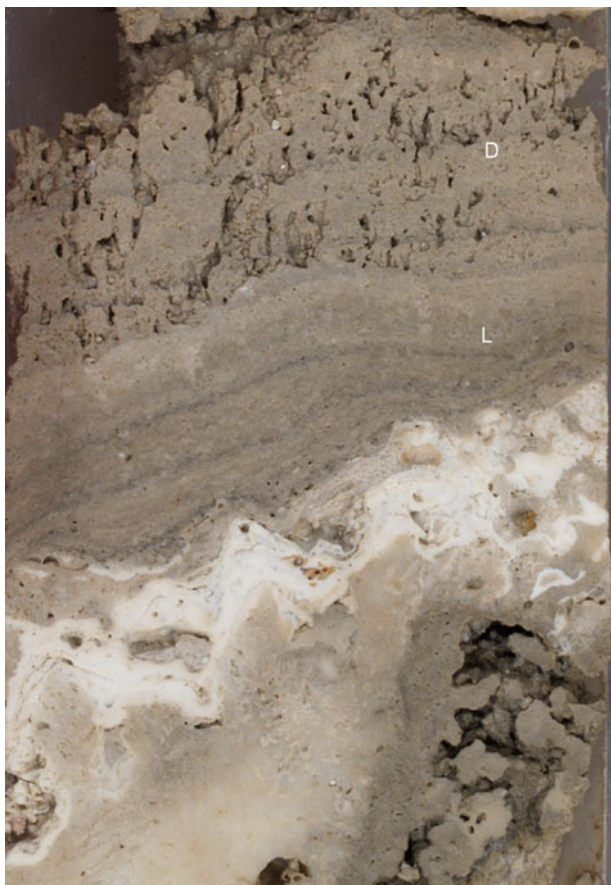
Crusts exhibit complex internal fine-grained microfabrics, with subordinate allochthonous grains and microencrusting skeletons. Silt-size grains made of fine-grained  $\text{CaCO}_3$  (peloids) are characteristic components of crusts (Macintyre and Marshall, 1988) (Figure 3). These grains, generally <50  $\mu\text{m}$  across, are relatively evenly spaced, and often 'float' in lighter colored microspar that includes irregular sinuous fenestrae up to 250  $\mu\text{m}$  across. Similar aggregates form geopetal fills in small cavities, and it appears that peloids occur both in situ precipitated crusts and as allochthonous (although probably quasi-autochthonous) fills.

### Origin

Even studies that described crusts as cements often invoked bacterial processes, such as decay of organic

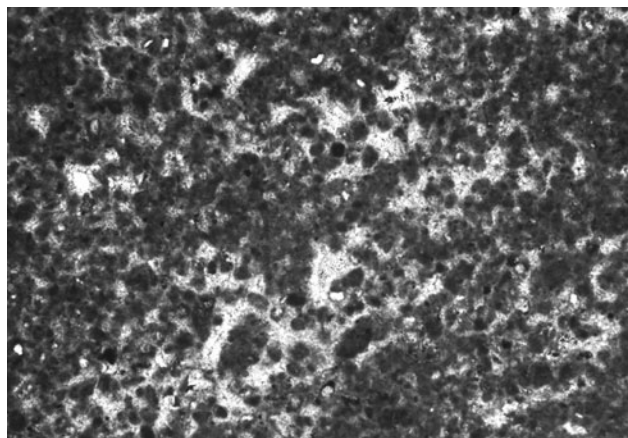


**Reefal Microbial Crusts, Figure 1** Fine-grained crusts (light) on dissolved vertical *Porites* branches (dark). Late Messinian (~5.5 Ma), Mesa de Roldán, Almería, SE Spain. The crusts have smooth external surfaces and range in thickness from ~3 mm to 3 cm.



**Reefal Microbial Crusts, Figure 2** Corallgal-microbialite reef framework with ~5 cm of fine-grained crust, showing laminated (L) lower part and dendritic (D) upper part. The crust overlies coralline algae (white) and other skeletal encrusters, which in turn overlie *Acropora* (bottom of picture). Core through late Pleistocene–early Holocene reef, SW Tahiti, IODP 310, Maraa eastern transect, Hole M0015B, Last Deglacial Sequence, Subunit 1B, interval 310-M0015B-19R-01, 59–67 cm (Camoin et al., 2007, p. 4, Figure F16). Visual core description and core images of Hole 310-M0015B. doi:10.1594/PANGAEA.499787. Width of view, 6 cm. © IODP/ECORD.

matter, to account for their formation (Macintyre, 1984, p. 232; Macintyre and Marshall, 1988). Chafetz (1986) proposed that peloids could form in semi-isolated cavities in present-day reefs by bacterially induced precipitation around suspended bacterial colonies. The presence of similar peloids, together with other microfabric comparisons (Riding et al., 1991; Montaggioni and Camoin, 1993; Zankl, 1993), and also the local presence of microbial filaments have all been used to infer a bacterial origin for the crusts. More specifically, their typically magnesian calcite composition, stable isotope values, and biomarkers provide evidence for sulfate-reduction: (a) Reefal peloidal crusts are typically magnesian calcites in the range 12–18 mole% Mg. Difficulties in obtaining such high Mg-calcite compositions inorganically suggest biological involvement such as



**Reefal Microbial Crusts, Figure 3** Peloid microspar microfabric, showing irregularly amalgamated dark peloidal masses in a light microspar, locally fenestral, matrix. Sample T302-R34, provided by Jody Webster; –988 m drowned reef, Kohala, NW Hawaii; approx. age 375,000–400,000 years. Width of view 1.4 mm.

bacterial sulfate reduction (Malone et al., 2001, p. 891, and Figure 10). (b) Bacterial processes, specifically sulfate reduction, have been inferred from carbon and oxygen isotope values of peloidal crusts and fills (Land and Goreau, 1970; Pigott and Land, 1986, Figures 9–11; Reitner et al., 2000, p. 153). (c) Reitner et al. (2000, pp. 158–159) found biomarker evidence for anaerobic heterotrophs in Lizard Island and St Croix peloidal crusts. In Tahiti reef crusts, Camoin et al. (1999, p. 297) found muramic and diaminopimelic acid, characteristic of bacterial cell walls, and Heindel et al. (2009) found fatty acids typical of sulfate reducers.

### Living examples

Living microbialites in reef caves are potential analogues for older crusts. Examples are centimetric crusts at Lizard Island and St Croix. These are forming in association with invertebrate and algal encrusters. Their surface microbial mucus can trap sediment and provide a medium for peloid precipitation (Reitner et al., 2000, pp. 154, 156). Chafetz's (1986) proposal that cavity peloids can be calcified bacterial aggregates is supported by the observation of organic remains in the cores of peloids forming in 'degraded microbial organic substances' within microbial films in St Croix caves (Reitner et al., 2000, p. 156, and Figure 5). Raised alkalinity in organic matrices associated with calcification in decaying sponges is 'believed to be largely a result of heavy sulfate reduction' (Reitner et al., 2000, p. 153).

### Sedimentological role

Thick crusts strengthen reef skeletons and reduce cavity volume, especially in branching or platy frameworks. In Messinian reefs of SE Spain, crusts up to 15 cm thick coat vertical *Porites* branches that are 1–3 cm wide and are linked horizontally by thinner platelike connections.



The crusts are therefore often thicker than the corals and locally constitute 80% of the reef volume. Crusts fused the otherwise delicate coral frame into a solid mass while the reef was still forming. The crust-welded reef rock occurs as cuboidal blocks up to 5 m across on the fore-reef slope (Riding et al., 1991). Crusts up to 20 cm thick occur in Late Pleistocene reefs in Tahiti (Camoin et al., 1999).

### Distribution and controls

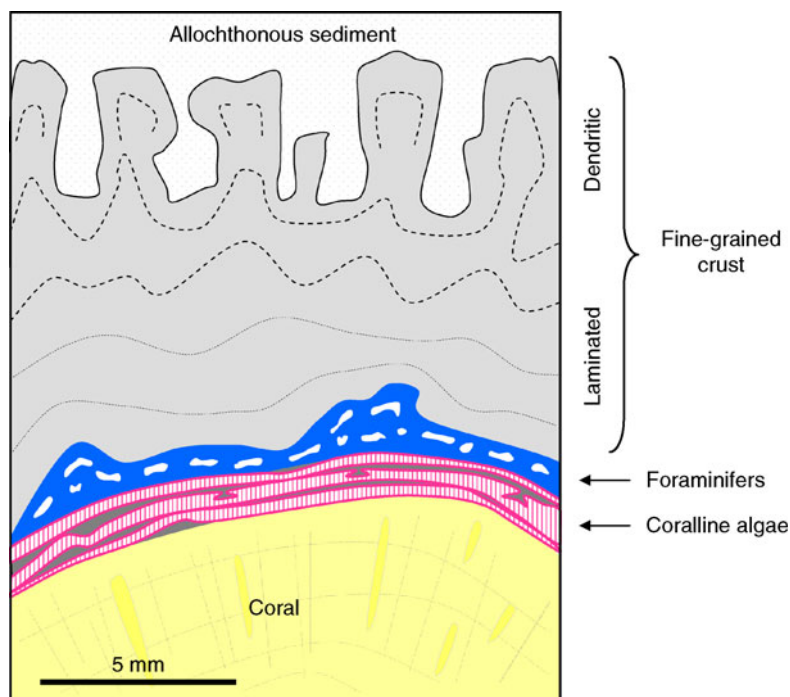
Crusts occur on wave-swept reef margins in enclosed framework cavities and on deep fore-reef slope surfaces. This is well documented from studies of Late Pleistocene–Holocene reefs (Macintyre, 1977, p. 513; Camoin and Montaggioni, 1994). Their formation in the closing stage of framework growth is reflected by their position between sciaphilic encrusters (e.g., corallines, foraminifers) and overlying reef or pelagic sediment. As light diminishes, reef surfaces are colonized by a succession of increasingly sciaphilic (shade-loving) skeletal organisms: coralline algae, bryozoans, sclerospores, foraminifers, and serpulids. The corallines can include shallower and deeper water communities (Braga et al., 2005; Webster et al., 2009, Figure 8). Fine-grained crusts typically overlie this sequence (Montaggioni and Camoin, 1993) (Figure 4). Crusts are preferentially developed on wave-swept margins, relative to lagoon and platform interior sediments, both in shallow reef crest zones (e.g., Macintyre, 1977) and on deeper foreslopes.

Ability to grow in dark environments is consistent with interpretation of the crusts as products of essentially heterotrophic bacterial communities. It also suggests contest for substrate in which crusts were outcompeted by eukaryote skeletal encrusts (see Eukaryote competition). Preference for wave-swept reef margins suggests the effect of seawater flushing on precipitation. This too is not inconsistent with a microbial origin for reefal crusts since bacterial calcification is strongly dependent on environmental factors that promote precipitation.

Late Quaternary crusts were common during deglacial sea level rise but declined ~6,000 years ago. This secular pattern of late Holocene decline was recognized in Tahiti and other Pacific reefs. A possible explanation is that crust formation was promoted by increases in alkalinity and nutrients in reef waters due to enhanced oceanic upwelling and terrestrial runoff during deglacial sea-level rise, and that these effects declined as sea level stabilized in the mid- Holocene (Camoin et al., 1999, p. 300).

### Eukaryote competition

The restriction of crusts to cryptic environments and deep foreslope habitats suggests competition for space with photophilic eukaryote reef builders. Such competition has long been considered a key factor in the geological decline of stromatolites in marine environments. Applying this view to reefal microbial crusts suggests that they were outcompeted for substrate by algal and invertebrate



**Reefal Microbial Crusts, Figure 4** Succession from coral to fine-grained crust: coral, coralline algae, foraminifers, crust. Variations are common; omitting some components and including additional skeletal encrusters. Based on Figure 2, and Riding et al. (1991, Figure 15), Riding and Tomás (2006, Figure 5), and Webster et al. (2009, Figure 8).



encrusters such as corallines and foraminifers. Only as decreasing illumination excluded even these shade-loving competitors did microbial crusts develop extensively. Relegation to dark habitats thus helps to account for crust development at the end of reef-growth. It also indicates independence of illumination, supporting an essentially heterotrophic interpretation of microbial crust communities.

### Fore-slope drowning

The formation of crusts in deepening sequences at the end of reef growth has been emphasized in studies of deep and drowned late Quaternary reefs. Late Pleistocene–Holocene crusts occur on reef foreslopes at depths of ~80–200 m in widespread locations, e.g., Jamaica, Belize, the Red Sea, Huon Gulf, Papua New Guinea, Tahiti and the Marquesas Islands, and Hawaii (Webster et al., 2009). It is not known whether these deposits are still forming. Presumably, they began to form during deglacial sea-level rise and are now at much greater depths than when they started. These deep ‘slope microbialites’ occupy a position between low-light framework encrusters, such as deep water corallines, and overlying pelagic sediments. Camoin et al. (2006, p. 289) suggested that crusts at Tahiti and the Marquesas Islands formed below 100 m because they overlie deep water assemblages of corallines and foraminifers, are partly contemporaneous with phosphate–FeMg crusts, and are overlain by planktic carbonates. Fore-slope crusts have therefore been regarded as signatures of sea-level rise (Camoin et al., 2006) and, in some cases, of reef drowning (Webster et al., 2009). The drowned reef at ~150 m around Hawaii shows shallow-water *Porites* overlain by sciaphilic skeletal encrusters, followed by microbial crusts (Webster et al., 2009, Figures 6, 8). The microbial crust is estimated to have formed at depths of ~120–150 m or more (Webster et al., 2009, 136–137). The sea-level rise that terminated reef development at this location can be connected to a deglacial meltwater pulse ~14,700 years ago (Webster et al., 2009, Figures 10, 11).

### Older examples

Fine-grained clotted-peloidal crusts are not restricted to geologically young reef corals. Similar examples have been widely recognized in skeletal reefs throughout the Palaeozoic and Mesozoic. Present-day reefal crusts can therefore shed light on the origin and development of much older examples. Early Cretaceous (120 million year) peloidal crusts on scleractinian corals have been interpreted as heterotrophic bacterial carbonates (Riding and Tomás, 2006).

Stromatolites and scleractinian corals can in several respects be regarded as end members of reef construction (Riding et al., 1991). Their locally intimate association in the Quaternary has implications for reef development and environmental change during this interval. The distribution of reefal microbial crusts in space and time, and the factors that have determined their development, are

significant research questions. Living examples need to be related in detail to Quaternary examples, and also to much older ones in the geological record.

### Acknowledgments

I am grateful to Juan Carlos Braga and Jody Webster for advice on the manuscript.

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## Cross-references

Microbes

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## REEFAL SEDIMENTS

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### Definition

A coral reef involves frame-building and frame-binding organisms, unconsolidated sediment fill, and the living veneer, which is an expression of the interactions between environmental and organic activities. Under normal conditions of stable sea level, the reef reflects a balance between the forces of construction (organic growth) and the forces of destruction (erosion, dispersal by transportation, and deposition).

Sediment production processes involve the mechanical and biological erosion of the cemented reef material and the decay/disintegration of the biogenic organisms in which the form of the skeletal material can be either segmented (*Halimeda*), tabular (red algae), or spicular (gorgonians, sponges, and holothurians), and the direct postmortem contribution of primary grains including whole tests of organisms such as foraminifera, small mollusks, and planktic calcareous or siliceous organisms, and the chemical and biochemical precipitation of discrete carbonate particles and cement.

The agents/controls are physical (waves) and currents, abrasion during transport, or biological such as rasping or burrowing organisms. Also, the decomposition of organic tissue may be assisted by bacteria and fungi. In several instances, growth characteristics dictate the skeletal particle size, e.g., benthic foraminifera. Population productivity may determine the initial distribution of the skeletal detritus, e.g., benthic foraminifera, coral, diurnal cycles in pH, dissolved CO<sub>2</sub>, and carbonate saturation may result in precipitation of calcium carbonate either as aragonite, high Mg-calcite, or calcite.

The result of the sediment production either remains in situ or undergoes transportation across the reef top to

the site of deposition. Large coral heads descend down the seaward slope or are thrown up onto the reef rim or reef flat. Coarse rubbles form prominent boulder zones, or coral sticks form conspicuous shingle ridges. Flat *Halimeda* plates form gravel deposits and benthic foraminifera concentrate in ponds or hollows. The sand-sized skeletal fragments are removed from the source area by currents of removal and are transported as bed load to be deposited in the sand wedge adjacent to the lagoon, and the finer sand and silt-sized material is transported in suspension to finally be deposited in the lagoon or carried to the leeward reef slope.

The processes of sediment breakdown can be differentiated into biological (disintegration), physical (attrition which is mechanical and disintegration through impact), mechanical breakdown into individual skeletal microarchitecture, or chemical/biochemical corrosion/solution and bacterial action. The agents/controls are the various organisms such as bottom feeders (sediment ingesters), rasps, grazers, crushers, and borers. The skeletal material thus produced is subjected to the variable energy experienced in the environment related to the strength and frequency of the waves and currents. In addition, the type, size, density, abundance of particles, and the mode of transportation (traction, saltation, and suspension) and the microarchitectural control further influence the relative abundance of particular particle sizes (Stoddart, 1969).

There is a continuous reduction of particle size. Discrete grain-size populations are produced either as skeletal modes or by discontinuous breakdown of the skeletal materials. There is greater fragmentation taking place in the traction load than in suspension. Also, there may be some degree of corrosion of the skeletal particles during passage through the gut of various organisms. In the high energy environments of the Great Barrier Reef, it is rare for fecal pellets to remain intact, and the finer-sized material within the pellets is dispersed by the currents and wave activity. Discontinuous size reduction of the skeletal material will finally produce very fine-grained sedimentary material, which takes the form of carbonate mud (finer than 0.03 mm). These muddy facies are restricted to the central part of the lagoons on the platform reefs, or the sediment wedge to leeward of the reef top.

The processes of transport are either biological (e.g., grazing by fish and turtles) or physical, which involves a winnowing process whereby sedimentary particles are moved in response to the normal physical transportation processes. In addition, very high energy but low frequency cyclonic activity provides an overprinting of the low energy, high frequency transitory waves and tidal currents. The sediments may be differentiated on the basis of particle size, shape, surface texture, and bulk density, and the interrelationship between roughness, threshold velocity, and settling velocity influences the relative importance of different transportation modes.

The effect/product of sediment transportation processes is that lag deposits remain in the high energy zone

near to their source. There is a gradual decrease in the grain size with increasing distance of transport. Eventually, there may be mixing of sediment from multiple sources and different energy regimes. The significance of textural variability is much more difficult to interpret than normal siliciclastic sediments and measurements such as particle size, skewness, standard deviation, and kurtosis that are complicated by the presence of distinct skeletal modes. Deposition is facilitated by the decrease in the velocity of the transporting current or by the influence of organic baffles such as sea grass or *Halimeda*. Some fine-grained sediment particles may be bound together by algal mats.

### Sediments of the Great Barrier Reef, Australia

Detailed studies of sediments from the reef tops of the Great Barrier Reef have been carried out by Maxwell and Swinchatt (1970), Maxwell (1973), Maxwell et al. (1961, 1964), Jell et al. (1965), Orme et al. (1974), Flood and Orme (1977), Jell and Flood (1978), Flood and Scoffin (1978), McLean and Stoddart (1978), Davies and West (1981), Smith et al. (1998), and Frank (2008).

The sedimentary facies may be differentiated on the basis of skeletal components or on the basis of their grain-size composition. There is a general correspondence between the distribution of the sedimentary facies and the morphological and the biological zonation. The reef rim, reef flat, sand wedge, and lagoon sediments display very distinct characteristics of both skeletal components and textural properties. Compositional variations are related to the different contributions of coral, coralline algae, benthic foraminifera, *Halimeda*, and mollusks. Five sediment compositional types have been recognized (Orme and Flood, 1980). Type 1 is high in corals and benthic foraminifera and it occurs at the outer margin windward reef flat and reef rim. Type 2 is high in coral content and occurs along the coral shingle ramparts and reef rim and toward the leeward part of the reef flat. Type 3 has a high percentage of coral and *Halimeda* and it is restricted to the more protected areas of the reef flat. Type 4 facies exhibit a high percentage of benthic foraminifera and it is located in hollows of the seaward extremities of the reef flat and reef rim. Type 5 facies contain a high percentage of *Halimeda* and it is restricted to the more protective part of the reef top such as in the lee of mangroves on the Low Wooded Island reef type.

Flood and Orme (1977) have explained how the general characteristics of the compositional sedimentary facies are related to the stage of morphological/evolutionary development of the reef type (see *Reef Classification by Maxwell (1968)*). The change in compositional sedimentary facies is related to the gradual replacement of reef building framework organisms by the surficial reef top epiphytic organisms such as the benthic foraminifera and plates which grow in the protected environments behind the mangrove vegetation.

There are four major textural types (Orme and Flood, 1980). Type 1 sediments are very coarse sands and gravels, moderate to poorly sorted, and consist predominately of coral and coralline algae. These sediments occur toward the outer windward margin of the reef flat and reef rim. They usually represent lag deposits remaining after wave and tidal action has removed the finer sedimentary particles. Type II sediments are very coarse or coarse sands, moderately well sorted, and consisting predominately of benthic foraminifera with a minor contributions or corals, coralline algae, and *Halimeda*. These sediments occur on the reef rim and the reef flat. Type III sediments are medium to fine sands, moderate to poorly sorted, and consisting of varying proportions of different organisms skeletal fragments. These sediments occur toward the leeward reef zone where sediment is reworked by tidal currents or in subtidal sediment bodies such as the sand wedge transitional between the reef top and the lagoon. Type IV sediments are very fine sands, moderately to poorly sorted, consisting predominately of very fine sand-sized coral fragments and other carbonate mid-sized material. These sediments occur mainly in lagoons on the lagoonal platform reefs where the lagoon acts as a sediment sink. On the platform reefs, this sediment type is transported from the reef top to the sediment wedge leeward of the reef top. The sedimentary texture of this type is principally related to deposition from suspension. These sediments commonly exhibit bimodal or multimodal size distributions that are a manifestation of varying high energy cyclonic events. Type I, II, and III sedimentary facies are transported principally by traction and saltation processes, whereas Type IV sedimentary facies are transported principally in suspension prior to settling. The average size where suspension is the main transportation mechanism is 0.125 mm; the average size where saltation replaces traction processes is 0.5 mm. The overall grain-size distribution is a reflection of the decrease in the energy available to transport sediment across the reef top.

A complex relationship exists between the biological components and the grain size Braithwaite (1973) and is produced by the irregular nature of the breakdown or disintegration of the individual skeletons (Sorby Principle). The following skeletal nodes have been identified within the sand sizes:

Coral (1.68–1.19 mm) and (0.105–0.062 mm),  
Foraminifera (1–0.59 mm larger species) and (0.149–0.125 mm, smaller species),  
Coralline algae (2–1.19 mm),  
*Halimeda* (1–0.125 mm),  
Mollusks (1.68–1.19 and 0.2 mm).

The analyses of the reef top sediments of the Great Barrier Reef show that sediments reflect the varying proportions of the skeletal elements present on the reef and that there exists a textural grain-size gradient from the windward reef margin to the leeward side. This gradient is a reflection of the diminishing wave energy available



for transportation of the skeletal particles. Sometimes, the lagoonal sediments appear to consist of discrete size modes that possibly reflect the rarer higher energy events (e.g., cyclones) more so than the various skeletal modes. Overall, the geomorphical/ecological zonation (reef rim, coral zone, cay, prograding sediment wedge, sediment blanket, shallow lagoon, deep lagoon, and windward vs. leeward reef flat) is reflected in the type of sediment, especially the textural type, more so than the skeletal compositional type. The differentiation of the textural type is a consequence of the environmental energy which influences erosion, transportation, and deposition.

### Sediments of Florida Reefs and Bahamian Reef

Ginsburg (1956) has described the environmental relationship of grain size and constituent particles in some south Florida carbonate sediments. He showed that the grain size and constituent particles reflect the submarine topography and hydrodynamics. Within the reef tract, the skeletal particle sediment constituents coarser than 1/8 mm are *Halimeda*, coralline algae, coral, foraminifera, and mollusks are the dominant skeletal organisms together with varying amounts of fine-grained carbonate sediment (very fine sand and mud-sized material).

Within the reef tract, the depositional environments are reflected in the particle size and constituent particles of their respective sediments.

### Sediments of the Belize Reefs

Macintyre et al. (1987) have described the Barrier Reef sediment apron of Tobacco Reef, Belize. In this reef setting, they have described distinct biological/sedimentological zones that parallel the reef structure. Their study showed that the sediments are transported from the reef crest and fore reef during periods of storms or hurricanes. The particle size of the sediments is largely a result of the differential transport by high bottom-water velocities during the high energy events. There is a positive correlation between the particle size and the distance of the sediment with respect to the reef tract. They recognized five distinct biological zones that paralleled the reef morphology and the back reef apron. They also report the occurrence of Mg-calcite precipitation in the reef lagoon (Macintyre and Aronson, 2006).

### Summary

The processes, agents/controls, and products of sediments of coral reefs have been summarized by Orme (1977). Whether it is the Great Barrier Reef, the Belize Reef, the Florida Reef, the Bahamas Reef, the mid-ocean atolls, the fringing reefs of New Caledonia, Indonesia, Hawaii, and so on, the same patterns of sediment production, sediment transportation, and sediment deposition apply (see Gishler, 1994; Gishler and Hudson, 2004). Irrespective of the different reef organisms that contribute to the source of the sediments, namely coral, coralline algae, *Halimeda*,

foraminiferans, mollusks, etc., the textural types of sediments are very similar in the reef slope, reef crest, reef flat, sand blanket, sand wedge, lagoon, or back reef of the different reef provinces. This reflects the similarity of the physical processes operating in the different environments and the different energy regimes which characterize the environments (Clack and Mountjoy, 1977; Stoddart, 1969).

The presence or absence of aragonite and/or Mg-calcite precipitates is a more vexing issue. Inorganic precipitation has not been conclusively demonstrated in the Great Barrier Reef, but it has been reported in the Belize Barrier Reef lagoon. In the instances where muds have been reported, their origin remains equivocal (Bathurst, 1975). The same can be said for the origins of "whittings," the possible spontaneous precipitates of aragonite, reported from the Bahamas and Persian Gulf. This issue requires further investigation.

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## Cross-references

Atolls  
 Barrier Reef (Ribbon Reef)  
 Cay Formation  
 Coral Cay Classification and Evaluation  
 Hydrodynamics of Coral Reef Systems  
 Reef Typology

## REEFS AT RISK: MAP-BASED ANALYSES OF THREATS TO CORAL REEFS

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## Definition

*Reefs at Risk* is a series of publications, produced by the World Resources Institute (WRI) in collaboration with partner organizations, that provides detailed spatial analyses of threats to the world's coral reefs.

*Reefs at Risk: A Map-Based Indicator of Threats to the World's Coral Reefs* (Bryant et al., 1998) was the first global, quantitative assessment of threats to coral reefs

ever conducted. Released in 1998, *Reefs at Risk* confirmed that coral reefs are seriously threatened in most parts of the world, clearly identified the human activities which threaten reefs, and called for global action. Over the last decade, the *Reefs at Risk* series – including regional analyses for Southeast Asia (Burke et al., 2002) and the Caribbean (Burke and Maidens, 2004), and local analyses for Sabah, Malaysia (Burke, 2003), and Belize (Burke and Maidens, 2005) – has stimulated public awareness, policy development, and scientific discourse. The series has been useful for conservation priority setting, and has shown decision-makers, politicians and the public where energy and resources should be focused to reduce critical threats.

The *Reefs at Risk* project series is led by WRI, but relies on a partnership with governmental and non-governmental organizations around the world. Partners are vital sources of data, provide guidance on the modeling methods, review model results, and contribute to the final report.

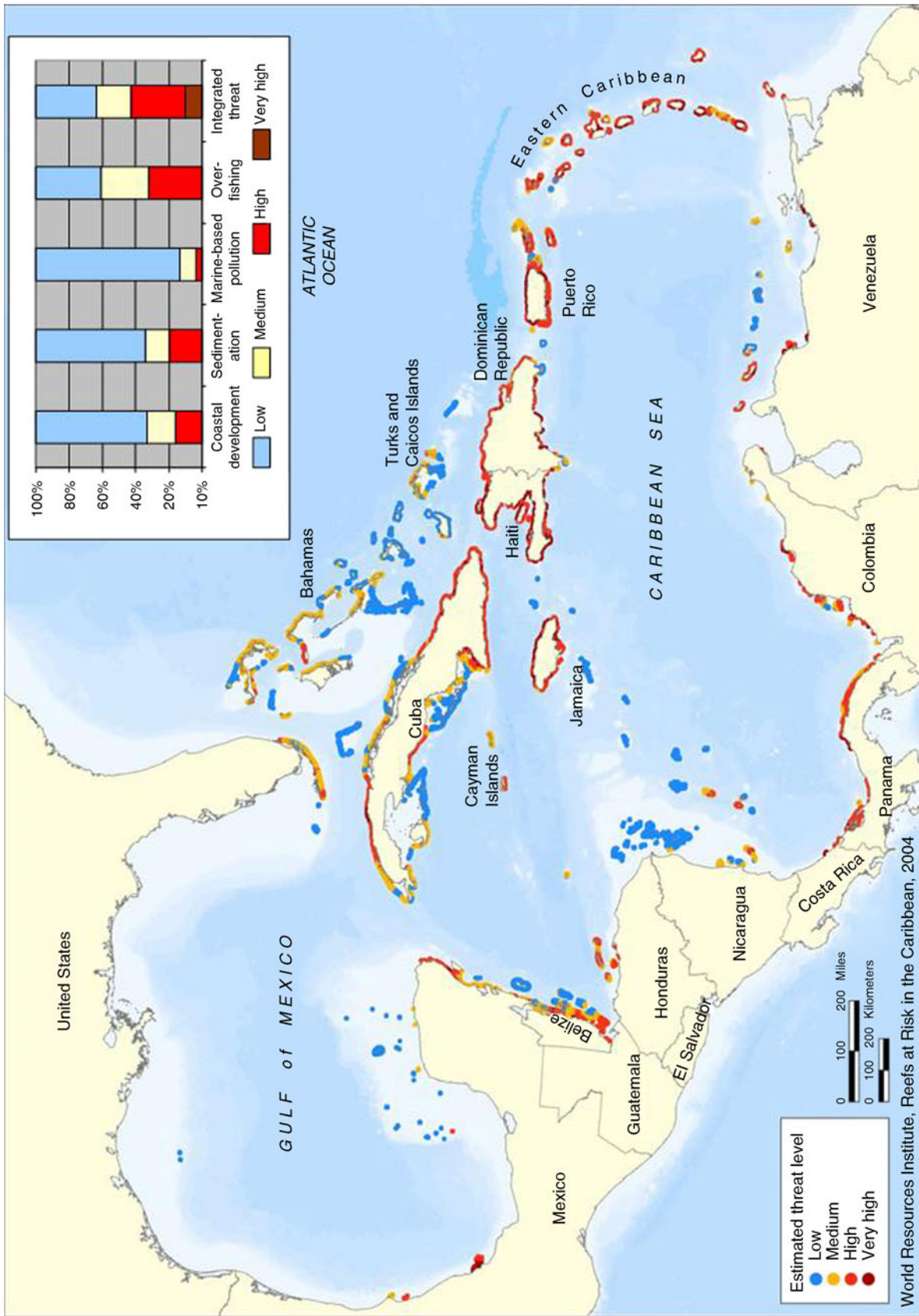
The core of a *Reefs at Risk* analysis is spatial modeling of human pressure on coral reefs within a geographic information system (GIS) framework. Indicators reflecting pressure on coral reefs from coastal development, watershed-based sediment and pollution, marine-based threats, overfishing, and destructive fishing are integrated into the *Reefs at Risk* threat index. Figure 1 provides an example of the typical representations of the integrated threat and level and source of pressures that underlie it.

The original global analysis, *Reefs at Risk: A Map-Based Indicator of the World's Coral Reefs*, uses a 4 km resolution coral reef data set. The regional analyses, *Reefs at Risk in Southeast Asia* and *Reefs at Risk in the Caribbean*, produced results at 1 km resolution. All project results (PDFs of reports and GIS data) can be downloaded from [www.wri.org/reefsatrisk](http://www.wri.org/reefsatrisk) or can be viewed in an interactive GIS at [www.reefbase.org](http://www.reefbase.org).

A new global analysis, *Reefs at Risk Revisited*, was initiated in 2008 and has a planned release in the fall of 2010. The analysis uses higher resolution data than the previous *Reefs at Risk* analyses, with coral reefs at 500 m resolution. It will also consider climate-related threats such as warming and acidifying seas, which were not included in the prior *Reefs at Risk* analyses. Project results will be available at [www.wri.org/reefsatrisk](http://www.wri.org/reefsatrisk) and [www.reefbase.org](http://www.reefbase.org), and data will also be available for viewing in Google Earth.

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**Reefs at Risk: Map-Based Analyses of Threats to Coral Reefs, Figure 1** Example of representation of threat and pressures in Reefs at Risk publications. Main section indicates "integrated threat" mapped for reefs of the Caribbean region. Inset is the Caribbean regional summary of 'integrated threat' (right column) plus the four pressures on which it is based: coastal development, sedimentation, marine-based pollution, overfishing.



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## Cross-references

Climate Change and Coral Reefs  
 Conservation and Marine Protection Areas  
 Mangroves  
 Nutrient Pollution/Eutrophication  
 Ocean Acidification, Effects on Calcification  
 River Plumes and Coral Reefs

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## REMOTE SENSING

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### Definition

Remote sensing is the collection of data without coming into physical contact with the target. In the field of earth, atmosphere and ocean observation, remote sensing generally refers to the use of imaging sensor technologies by ways of aircraft, satellites, ships, and buoys. The target information is carried to a sensor by the electromagnetic radiation or by acoustic sound waves.

### Introduction

Coral reef structures and processes span a large range of spatial scales, from microscale to planetary scale. Smallest scales can be observed in vitro in laboratory and aquaria and in situ. Instruments (such as microscopes, probes, lasers, x-rays, cameras, coring devices, and many others) and visual observations are used in reef geology, physiology, biology, and ecology to elucidate the processes regulating the life of coral reef organisms and the formations of coral reefs. However, above the scale of few tens of meters, it is impossible to measure directly and completely a phenomenon with these techniques. It becomes necessary to sample throughout the spatial domain to acquire representative observations and rely on statistics to estimate means, standard deviations, and probabilities. Often, laboratory and in situ observations cannot be repeated frequently due to costs and logistical limitations to access field sites.

Remote sensing provides the means to make measurements synoptically on reefs, at large spatial scale. This macroscope can be used to scale up field observations. Remote sensing often offers repeatedly acquired data, spanning several decades in some cases. This now provides the most objective basis to assess anthropogenic and climate change effects on a variety of ecosystems. However, there are many technological and

environmental limitations in the type of observations that can be acquired remotely.

Two domains characterize reef remote sensing: the sensing of the reef itself, with its submerged living communities and its carbonate framework and the sensing of the reef physical, chemical, and biological boundary conditions made by the ocean, the atmosphere, and the land masses. Sensus Andréfouët and Riegl (2004), reef sensing and reef environment sensing are respectively direct and indirect reef remote sensing. These approaches have different spatial and temporal focus. They use different types of sensors and technologies adapted to different parts of the electromagnetic and acoustic spectrum.

### Electromagnetic and acoustic spectrum

Radiation across the entire electromagnetic spectrum can be used in remote sensing technologies with increasing wavelength and these are the ultra-violet (0.3–0.4 micrometers [ $\mu\text{m}$ ]), the visible (from blue to red light, 0.4–0.7  $\mu\text{m}$ ), the infrared (0.7–3  $\mu\text{m}$ ), the thermal infrared (3–15  $\mu\text{m}$ ), the far infrared (15–1,000  $\mu\text{m}$ ), and the microwave radiation (above 1,000  $\mu\text{m}$  or in the more common frequency unit used for microwave radiation, 1 giga Hertz [GHz]). Acoustic in-water systems operate at a much lower frequency, between 10 Hz and 1 MHz (Rees, 2001).

### Categories of remote sensing systems

A sensor and its deployment platform (which can harbor several sensors) constitute a remote sensing system. The type of radiation used, frequency of acquisition, platform altitude, and orbit (sun-synchronous, polar, geostationary, etc.) define a system. In addition, a remote sensing mission would also comprise parameters such as energy and life expectancy, recording devices, data transfer and ground receiving stations (for satellite sensors), acquisition scheduling, on-board and on-ground calibration systems, and software and data distribution for end users. Missions are too numerous to describe them exhaustively here, and they have a limited lifetime, thus information can become rapidly obsolete. However, some missions have been maintained over several decades by the repetitive launch of a series of satellites carrying sensors with consistent specifications. This is the case of Landsat 4, 5, and 7, SPOT 1-3, and the NOAA-POES (Polar Operational Environmental Satellites) series of satellites that were initiated respectively in 1982, 1986, and 1978. Remote sensing textbooks (Jensen, 2006; Lillesand et al., 2007; Campbell, 2008) and internet resources often provide a listing of ongoing, past, and sometimes future missions ([http://en.wikipedia.org/wiki/List\\_of\\_Earth\\_observation\\_satellites](http://en.wikipedia.org/wiki/List_of_Earth_observation_satellites)). Table 1 refers to the most common systems used for coral reefs.

Missions are generally government endeavors due to their very high planning and operating costs, but some have also been conceived by private commercial companies such as Orbimage, DigitalGlobe, and GeoEye.

**Remote Sensing, Table 1** Overview of most common remote sensing platforms, sensors types, and applications relevant to coral reef science and management

| Platform                                       | Ship     |       |           | Aircraft          |                 | Satellite                       |                             |           |              |       |                              |                                              |
|------------------------------------------------|----------|-------|-----------|-------------------|-----------------|---------------------------------|-----------------------------|-----------|--------------|-------|------------------------------|----------------------------------------------|
|                                                | Acoustic | Laser | VHR Lidar | VHR hyperspectral | VHR photography | Visible infra red hyperspectral | VHR infra red multispectral | Quickbird | Landsat ETM+ | MERIS | Thermal infra red radiometer | Active microwave scatterometer and altimeter |
| Example of sensor                              | QTC view | FILLS | EEARL     | CASI              | Digital camera  | Hyperion                        | Quickbird                   |           |              |       |                              |                                              |
| Species identification                         | n        | n     | n         | n                 | n               | n                               | n                           | n         | n            | n     | n                            | n                                            |
| Coral cover                                    | n        | p, ?  | n         | p                 | p               | ?                               | p                           | p         | n            | n     | n                            | n                                            |
| Benthic Communities                            | <10      | p, ?  | <10       | <30, ?            | <30             | ?                               | <30                         | <30       | <10          | n     | n                            | n                                            |
| (< number of classes)                          |          |       |           |                   |                 |                                 |                             |           |              |       |                              |                                              |
| Community changes                              | p, ?     | p, ?  | p, ?      | p                 | p               | ?                               | p                           | p         | p            | n     | n                            | n                                            |
| Bathymetry                                     | y        | y     | y         | p                 | p               | p, ?                            | p                           | p         | p            | p     | n                            | n                                            |
| Rugosity                                       | y        | y     | y         | p                 | p               | p, ?                            | p                           | p         | p            | n     | n                            | n                                            |
| Fine geomorphology                             | p        | p     | y         | y                 | y               | p, ?                            | y                           | y         | n            | n     | n                            | n                                            |
| Coarse geomorphology                           | n        | n     | y         | y                 | y               | y                               | y                           | y         | y            | p     | n                            | n                                            |
| Measuring coral bleaching (direct)             | n        | ?     | n         | p                 | p               | ?                               | p                           | p         | n            | n     | n                            | n                                            |
| Monitoring coral bleaching (indirect)          | n        | n     | n         | n                 | n               | n                               | n                           | n         | n            | n     | y                            | n                                            |
| Monitoring water quality (indirect)            | n        | n     | n         | n                 | n               | p, ?                            | n                           | n         | n            | y     | y                            | n                                            |
| Monitoring sea surface, wind, waves, and tides | n        | n     | n         | n                 | n               | n                               | n                           | n         | n            | n     | n                            | y                                            |
| Monitoring sea surface height                  | n        | n     | n         | n                 | n               | n                               | n                           | n         | n            | n     | n                            | y                                            |

*Note:* *VHR* very high spatial resolution (<10 m); *HR* high spatial resolution (10–30 m); *MR* medium spatial resolution (30–300 m); “n” not possible; “y” routinely possible; “?” the potential is not fully evaluated, p: has been demonstrated in a limited number of cases, thus possible but warrant further investigations. For “Benthic communities,” an order of the number of classes that can be mapped is provided. However, this is highly site dependent and processing dependent and not necessarily just a function of the sensor. “Fine geomorphology” characterizes structural features of few tens of meters, like spur-and-grooves, crests, small patches, reticulated formations, navigation channels. “Coarse geomorphology” characterizes the identification and mapping of hundreds-of-meters-sized structures such as fringing, patch, and barrier reefs. At this scale, shipborne platform is not suitable. “Measuring coral bleaching” consist in evaluating during a bleaching event the portion of the reef, or the portion of the live coral, that is bleached. “Monitoring water quality” using multispectral satellite is possible but with a limited repeat time. *ASCAT* Advanced Scatterometer on board the MetOp-A satellite; *OSTM* Ocean Surface Topography Mission on board the Jason-2 satellite. Other acronyms: see text. Other information are available in Mumby et al. (2004)

This economic sector has proven highly successful since the launch of the first commercial spaceborne sensor (IKONOS) in 1999. Very high resolution commercial remote sensing is also an important contributor to scientific applications (Goward et al., 2003). Acoustic systems are widely operated by private sector companies.

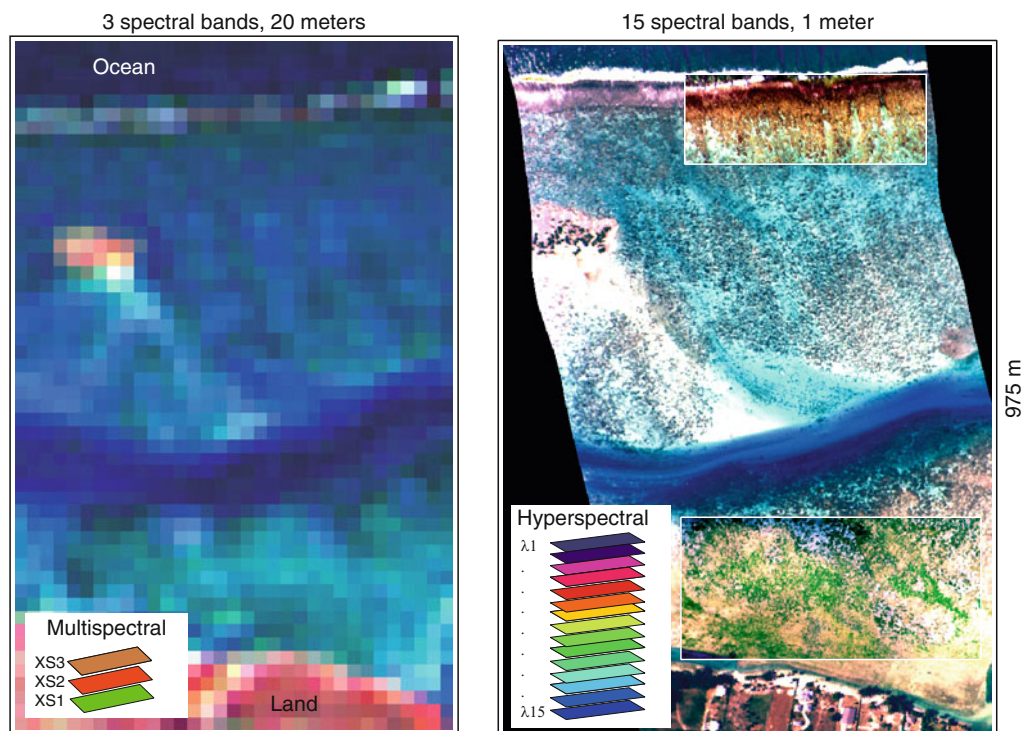
Remote sensing sensors can be classified in several ways. Useful distinctions are between passive and active sensors and between imaging and nonimaging systems.

Passive sensors detect the radiation emitted or reflected by the target, typically the emitted thermal infrared and the reflected sunlight. Typical passive sensors include film photography, charged coupled devices in cameras, and radiometers. Active systems emit radiation to scan the target and measure the signal reflected or backscattered by the target. A third distinction useful in active systems is between ranging and scattering techniques. Ranging focus on the time delay between transmission and reception of the signal, whereas scattering techniques focus on the strength of the return signal, although both time delays and strength can be used by the same system. Typical are laser-based systems (e.g., LIDAR, standing for Light Detection and Ranging) working in the visible part of

the spectrum, and RADAR systems (Radio Detection and Ranging) working with microwave radiation. This includes scatterometers, altimeters, profiling radars, and synthetic aperture radars.

Acoustic active SONAR (Sound Navigation and Ranging) systems use sound wave propagation in the water to sense the bottom and are not limited by depth, except in very shallow waters. Frequencies and sensors are adapted to the depth range of the study area. Side-scan sonars and single-beam and multi-beam echo sounders have been used principally for depth measurements, but they also provide bottom discrimination capabilities, hence several systems are referred to as Acoustic Ground Discrimination Systems (AGDS).

Imaging sensors (active or passive) produce a two-dimensional (2D) array of information by, for instance, using a 2D matrix of individual sensors (such as charge coupled devices or digitized film photography) or by using 1D sensor and the motion of the platform to scan the target. The interest of imaging systems is to produce a swath measurement, a pictorial representation of radiation as a function of position on the target. Imaging systems are used to create maps of the targeted portion of the Earth surface.



**Remote Sensing, Figure 1** Examples for a nearly 1-km-wide flat reef of the information provided by: (left) a high-resolution (20 m), multispectral, spaceborne sensor like SPOT-HRV and (right) a very high spatial resolution (1 m), hyperspectral, airborne sensor like CASI. Hyperspectral data offers the possibility to work with the most useful bands, for instance, to map brown algae biomass on the reef crest (upper rectangle) or a green algal bloom occurring on the fringing reef (lower rectangle).



### Spatial, spectral, and temporal resolutions

From a user standpoint, systems and remote sensing images can be usefully characterized by at least their spatial, spectral, and temporal resolutions. Figure 1 compares, for the same site, images at different spatial and spectral resolution.

A consequence of the field of view of the sensor and its altitude, the spatial resolution, is the size of the area on the target covered by each sampling unit. In other words, it is the size on ground of the pixel (picture element) of the digital image. This is different to the minimum discernible unit (MDU), which is larger than the spatial resolution: a 1-m spatial resolution sensor will not discriminate 1-m-size objects, but at best 2–3 m-size objects. The MDU limit is inherent to the sensor, but also dependent on environmental and geometrical conditions at the time of the acquisition and the type of processing and resampling that is applied to the image, for instance, to correct for geometric distortion.

The spectral resolution is defined by the number and width of the portions of the electromagnetic spectrum measured by the sensor. These so-called spectral bands are defined by their positions (center, width) and by their sensitivity curves. Panchromatic and multispectral sensors dominate passive optical sensors. Respectively, they provide one large and up to four narrow spectral bands in the visible range. Hyperspectral sensors provide up to several tens of nonoverlapping narrow bands in the 0.4–0.7- $\mu\text{m}$  visibility. Unfortunately, they are still limited to few airborne deployments worldwide. In 2010, only one high spatial resolution hyperspectral sensor was launched into space (Hyperion), and one medium spatial resolution (300 m) 15-band sensor (MERIS).

The temporal resolution is the minimum time interval between two acquisitions of the same target. These acquisitions can be real or virtual depending on the mission scheduling of acquisitions. Low resolution sensors such as SeaWiFS or MODIS may acquire data at every opportunity with a revisit time of only 1–2 days, while high-resolution sensors such as Landsat ETM+ or SPOT HRG need to be programmed and data are acquired only on demand. For instance, the Landsat satellite revisit time is 16 days, but images may be acquired only once a year (Arvidson et al., 2001). Geostationary sensors look at their target continually, thus revisit time can be as often as required. Commercial sensor providers have an on-demand strategy, but they have also built systematic quasi-global archives of images which will be extremely useful in the case of detection of change.

### The infrared limit

Radiations at wavelength higher than the infrared cannot penetrate water bodies by much more than 1 m in the best case. Quickly, they provide only surface skin information. Since they also provide information on the atmosphere

above the water, and on the land masses, they can be of use when studying coral reef processes influenced by atmospheric and terrestrial processes and cannot be neglected for indirect reef remote sensing. Much information can also be gained within these wavelengths when applied to exposed reef flats at low tide.

At shorter wavelength than the infrared, incident light can penetrate the water, and an upwelling water-leaving radiance signal coming from the water column can be measured by a surface, airborne or spaceborne, downward-looking sensor. The physical and biological interpretation of this radiance signal requires an understanding of the radiative transfer theory. Radiative transfer characterizes the change in direction and intensity of radiation in the air, in the water, and at their interface, due to inherent (absorption, scattering) and apparent optical properties (reflectances, diffuse attenuations, and inelastic scattering like fluorescence). For optically shallow water of depth  $z$ , the water column and the bottom signal that can be measured at the sensor level depend on the incident light, the water optical properties, the reflective and scattering properties of the bottom, the air–sea interface, and the atmosphere (Mobley, 1994; Kirk, 1994). Maritorena et al. (1994) present in a remote sensing context a useful analytical model for optically shallow water when the bottom contributes to the surface signal. It is much more difficult to characterize water optics and interpret images with radiative transfer equations in shallow coastal environments than in the deep ocean, since products in the water can typically have various origins and nature (phytoplankton, colored dissolved organic matter, particulate organic and inorganic matter).

### Processing

Because remote sensing is based on the characterization of electromagnetic radiation and sound waves, data processing relies on a physics-based approach to identify the target signal among the other environmental signals that can be considered as noise. In principle, physics-based algorithms imply site-independent and globally valid processing methods. Applying radiative transfer equations should, in principle, provide the radiometric (or acoustic if sound wave propagation equations are used) value of the target and thus allow its identification. However, in practice, there are many limits to this approach. First, it is not always feasible to accurately solve radiative transfer equations, because there may be too many unknowns in the equations. A solution would be to deploy in situ instruments to acquire, for instance, in-water optical data at the time of the remote sensing acquisition, but this is often unpractical. The second and most important reason is that a radiometric or acoustic value, even if precisely estimated, does not necessarily have a meaning and an immediate interest in terms of ecological, biological, or geological process. In these thematic domains, empirical statistics are often necessary to

define thematic objects of interest, especially for the large objects that could be identified at a size consistent with the spatial resolution of the sensor (living communities, habitats, carbonate structures). Thus, to make the connection between the information contained on the image pixel and the statistically defined ground information, statistical processing of the images is often enough, without the need to fully characterize the electromagnetic signal. In this processing, the output information is not the absolute precise physical signature of any given pixel, but rather the fact that a cluster of similarly colored pixels are significantly different than another cluster. Statistical processing offers a large panel of image-based techniques based on pixel color and spatial configuration (supervised and unsupervised classification, hard and fuzzy classification, segmentation, texture). It is typically a site-dependent, image-dependent processing. The physics-based and statistics-based approaches have been named “reef-up” and “sensor-down” approaches respectively (*sensu* Hochberg et al., 2003; Purkis, 2005).

Recent method development applied to the direct or indirect reef remote sensing is computational intelligence (Ressom et al., 2005). These mathematical models come from the Artificial Intelligence field to extract knowledge from large data sets, to solve optimization problems, and to transform human expert knowledge into mathematical description and algorithms. It includes, among the most frequently encountered techniques, neural networks, genetic algorithms, and fuzzy logic systems. Present applications are limited to water quality analysis in coastal waters and habitat mapping, but this is likely to increase in the future.

Practically, most modern applications rely on a combination of the physical, statistical, and computational intelligence approaches. Typically, the physics-based processing provides images radiometrically corrected to have consistent radiometric information for multi-images, multi-temporal, and multi-site comparisons. Statistical processing is then used to extract thematically relevant information from the calibrated images. Finally, computational intelligence methods and expert knowledge can be used to refine an analysis, if errors and possible improvements have been detected. This mix of approaches is useful for both direct and indirect remote sensing.

### **Spectral signatures and the hyperspectral potential**

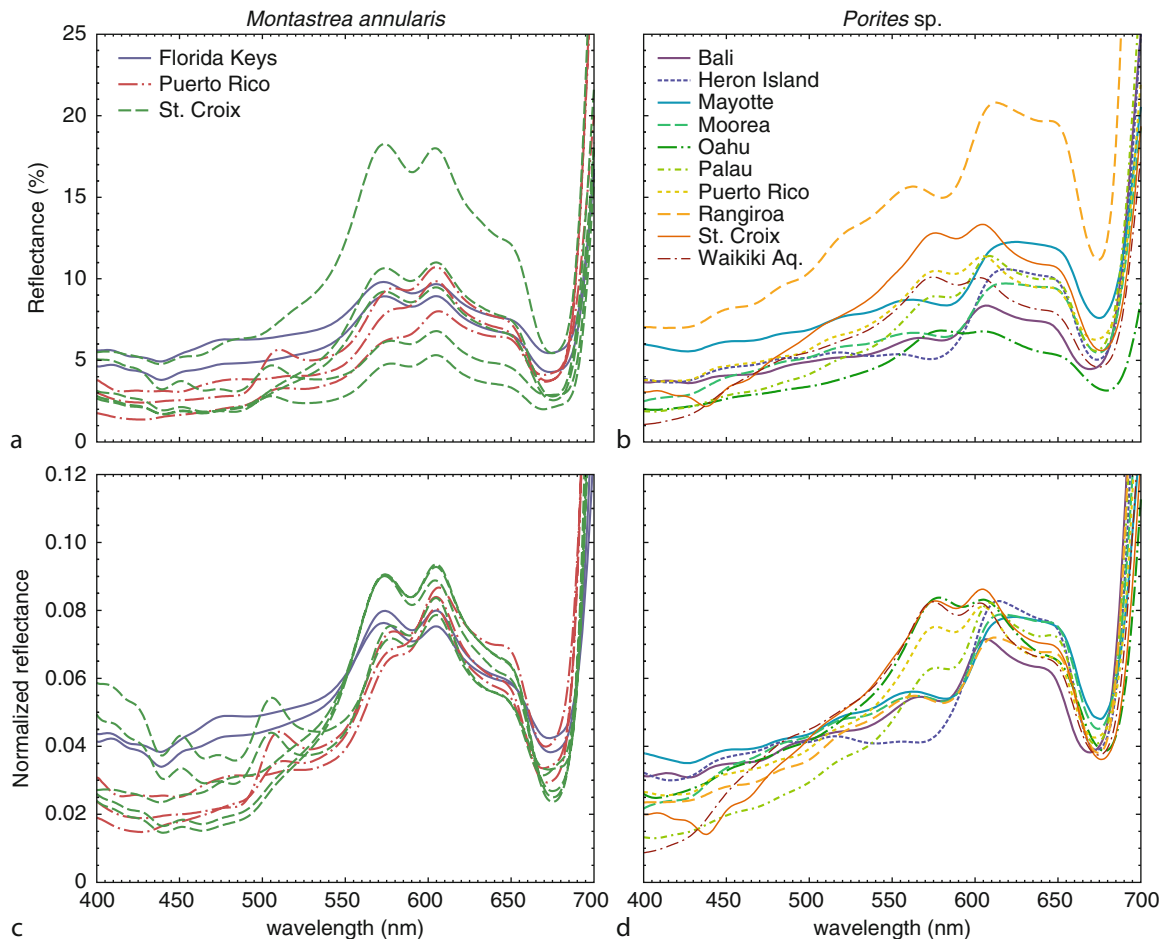
With the emergence of numerous airborne hyperspectral sensors in the early years of the 1990s, marine imaging spectrometry developed quickly, including for shallow waters and coral reefs. Areas covered by airborne hyperspectral surveys in the years 1995–2010 include selected reefs in Mauritius, La Réunion, Turk and Caicos, Florida, Bahamas, French Polynesia, Hawaii, Japan, Virgin

Islands, Puerto Rico, Belize, Australia, Seychelles, and Indonesia. Sensors include, but are not limited to, AVIRIS (Airborne Visible Infrared Imaging Spectrometer), MASTER (MODIS/ASTER Airborne Simulator), CASI (Compact Airborne Spectrographic Imager), AISA (Airborne Imaging Spectoradiometer for Applications), PHILLS (Portable Hyperspectral Imager for Low Light Spectroscopy), and HYMap (Hyperspectral Mapper). Note that one acronym may represent several versions of an instrument, as these high-technology devices are continuously enhanced. Hyperspectral airborne studies have been generally paralleled by the acquisition of spectral signatures on the ground.

Spectrometry focuses on the collection and characterization of continuous spectra acquired in laboratory (reflectance), in situ with portable and sometimes waterproof radiometers (radiance reflectance), and by remote sensing (remote sensing reflectance). Spectra are analyzed in intensities and shapes according to the absorption features partly due to the pigment compounds of the target (Hedley and Mumby, 2002). This target is often made of a mosaic of centimeter-scale “pure” constituents. Representative spectra of these constituents (the so-called end members) form a spectral library that can be used in theory to interpret hyperspectral remote sensing images using radiative transfer equations, in order to create, for instance, a map of living communities for the targeted reef. However, these end members do not necessarily have just one “representative” spectrum (e.g., for corals, see Figure 2 and Hochberg et al., 2004). Furthermore, since similar pigments can be found in a large variety of organisms, discriminant spectra for every biological end member may not exist (e.g., for hard coral, soft coral, fleshy algae, turf algae, colonized rubble, microbial mats [Hochberg et al., 2003]). Finally, on the ground, these end-member spectra merge at the scale of few centimeters given the high patchiness of benthic cover in coral reefs. Effective and routine spatial and spectral unmixing of end-member spectra from image acquisitions remain a future target at this stage. These considerations have complicated the automatic processing of hyperspectral images, even with the most recent and performing optimization techniques (Lee et al., 2001).

In fact, simulations have shown that a multispectral sensor with less than 10 bands with adequate spacing and width would be ideal for reef studies (Hochberg and Atkinson, 2003). Although a number of space missions dedicated to coral reefs have been discussed, none of them was funded beyond preliminary feasibility studies. To date, the only high spatial-resolution missions with a dedicated coral reef acquisition plan are the Landsat 7 mission and the collection of digital photographs taken from the International Space Station by astronauts (Arvidson et al., 2001; Robinson et al., 2006).

Despite confounding signatures and the absence of a nongovernmental very high spatial resolution



**Remote Sensing, Figure 2** Variability in spectral signatures (reflectance  $R$ ) of corals, specifically for *Montastrea annularis* and *Porites sp.* Panels (a) and (c) show mean absolute and normalized  $R$ , respectively, for ten colonies at three sites in the Caribbean. Panels (b) and (d) show mean absolute and normalized  $R$ , respectively, for ten sites around the world (b). (Data from Hochberg et al., 2004.)

hyperspectral spaceborne sensor in 2010, hyperspectral data and spectrometry remain a promising field for coral reef investigations. It is predictable that near-future on-demand availability of affordable hyperspectral data will quickly transform the field of direct coral reef remote sensing.

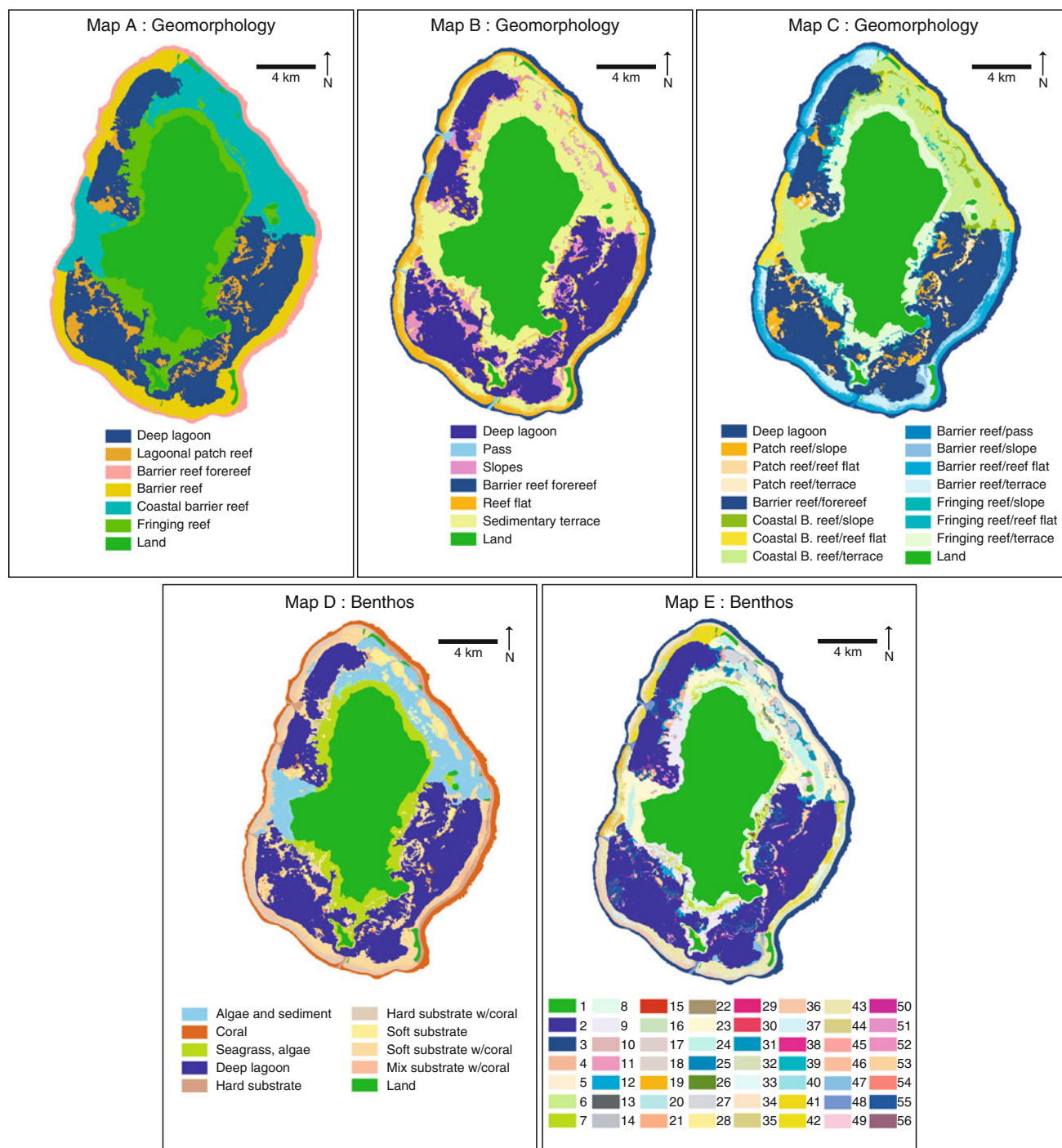
### Past and current application of optical passive sensors for direct reef remote sensing

For direct remote sensing, down-looking, passive optical remote sensors in air and space provide data in the blue-near infra red part of the spectrum that are useful for coral reef observations. These optical data have vastly dominated, and still dominate, the field of direct coral reef remote sensing. Historically, airborne photography cameras were first used, followed by high-resolution, spaceborne, multispectral sensors (on board the various Landsat, SPOT, IRS spacecrafts) in the 1980–1990s, then

airborne hyperspectral sensors (such as AVIRIS, CASI, AISA, PHILLS) in the 1990s, followed by the emergence of very high resolution, spaceborne, multispectral sensors (on-board IKONOS, Quickbird, FORMOSAT, GEOYE 1, SPOT-5, Orbview-4). Aerial photography and multispectral spaceborne sensors remain the most frequent data source. The very high spatial resolution commercial sensors are increasingly used, given their interesting resolutions compared to other sensors, but they remain often limited to small-scale projects, for a particular site (Mumby and Edwards, 2002; Andréfouët et al., 2003; Capolsini et al., 2003).

Main applications are listed in Table 1. The dominant application is habitat and community mapping (Figure 3), then bathymetry modeling, itself a necessary part of benthic rugosity assessment. These applications still remain actively pursued research and management topics, since the achieved accuracy is not necessarily very high (Mumby





**Remote Sensing, Figure 3** Examples of geomorphology and benthic maps achieved for Wallis Island using digitized aerial photographs. Different types of maps can be produced depending on the applications. All these maps can be considered as habitat maps, displaying different thematic resolution. *Map E* is the most complex, with 56 classes. (Details in Andréfouët, 2008.)

et al., 2004; Knudby et al., 2007; Lyzenga et al., 2006; Andréfouët 2008; Minghelli-Roman et al., 2009). It is predicted that the number of applications involving the detection of changes will grow, often by combining

different image sources, including aerial photographs, to span the longest possible period (Scopélitis et al., 2009). Finally, it must be pointed out that the elaboration of remote sensing products is frequently not anymore the final goal

and focus of the most recent published study (Andréfouët and Riegl, 2004). Publications become much more user oriented than producer oriented. Interdisciplinary studies taking advantage of remote sensing capabilities and products are increasing, for instance, in geology, ecological modeling, monitoring sampling design, biodiversity applications, conservation planning, and fishery management (Gilbert et al., 2006; Pittman et al., 2009; Purkis et al., 2008; Riegl et al., 2007; Green et al., 2009).

### **Past and current application of acoustic and optical active sensors for direct reef remote sensing**

Active in-water acoustic systems operated from small boats are increasingly used, partly because optical data are quickly limited by depth and turbidity and partly because acoustic systems provide precise bathymetric data that can be used to correct optical data for water column attenuation effects. However, acoustic data are useful for their own sake, to measure depth, identify bottom features and map habitats, although they cannot resolve as many habitats as optical data would do. Most common AGDS sensors are RoxAnn<sup>®</sup>, Qeuster Tangent Corp (QTC)-View<sup>®</sup>, and ECHOpus<sup>TM</sup>. A full review of past coral reef applications is provided by Gleason (2009). The predicted trend is to see a better synergy between acoustic and passive optical acquisitions for local scale applications (Riegl and Purkis, 2005).

Although still fairly uncommon due to costs of data acquisition, the active airborne lidar systems have proven their utility (Brock and Purkis, 2009; Costa et al., 2009). Extensive data sets exist in waters under United States jurisdiction (e.g., Hawaii, Florida, Puerto Rico, Virgin Islands) and over the Great Barrier Reef, acquired with SHOALS (Scanning Hydrographic Operational Airborne Lidar Surveys), EAARL (Experimental Advanced Airborne Research Lidar), and LADS (Laser Airborne Depth Sounder) systems. Data collection occurred in 2009 in the Indian Ocean coral reefs under French jurisdiction. Lidar accurately provides bathymetric data that can be acquired, as another major advantage, simultaneously with optical data if a camera or radiometer is on the same platform (Brock et al., 2004). Lidar data have been processed to extract rugosity information, which is a key habitat descriptor, for instance, to explain and predict the distribution of fish communities (Pittman et al., 2009).

Finally, in-water laser-induced fluorescence deployed at night with the FILLS (Fluorescence Imaging Laser Line Scanner) has been successfully tested to map reef communities, at a spatial resolution of a few centimeters. However, this has remained experimental and has not been generalized (Mazel et al., 2003).

Similar to passive optical data, active remote sensing products are now directly used in thematic studies relevant to fishery management, geology, biodiversity, and species–habitat relationships, and marine protected areas (e.g., Kuffner et al., 2007; Gleason, 2009).

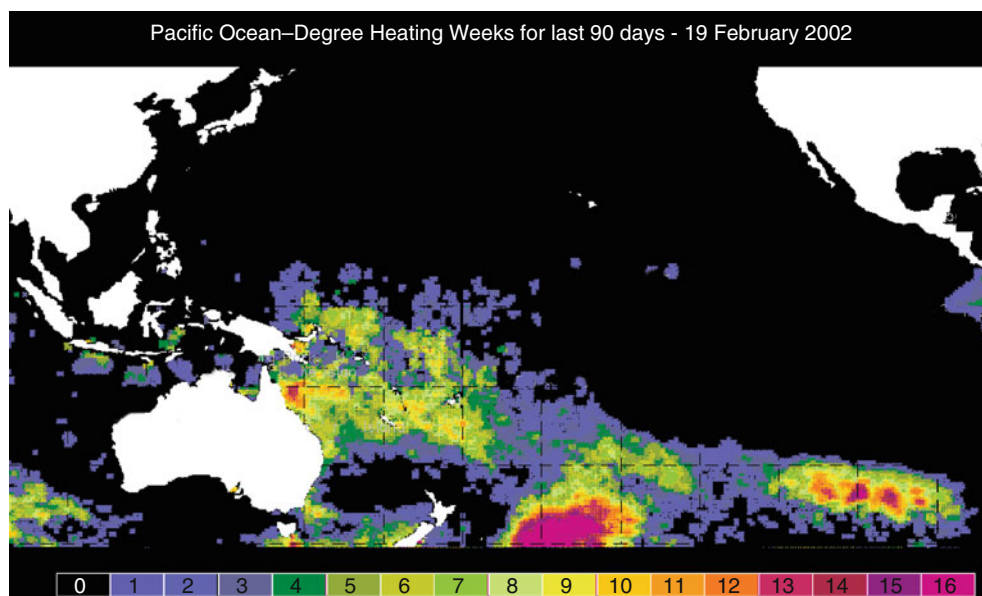
### **Past and current application of thermal infrared passive sensors for indirect reef remote sensing**

Thermal infra-red data have been used for indirect remote sensing of reefs since the 1990s, especially using the AVHRR (Advanced Very High Resolution Radiometer) sensors that provide Sea Surface Temperature (SST) (Gleason and Strong, 1995). In the wake of the coral bleaching events related to strong El Niño and positive thermal anomalies in 1998, SST-derived proxies have been much more intensely used to forecast coral bleaching. Warnings are issued by the NOAA Coral Reef Watch project whenever the critical threshold of warming stress is approached. The threshold depends on the stress index used, for instance, the global Degree Heating Weeks (Figure 4). Local indices exist, such as Max3d, which was identified for the Great Barrier Reef (Berkelmans et al., 2004). The validity of these SST-based proxies is under discussion, especially in the light of their coarse spatial resolution (0.5° or roughly 50 km, worldwide), compared to the spatial patchiness at which bleaching occurs. Another discussion topic is the refinement and validation of the issued forecasts using ancillary environmental and biological data (McClanahan et al., 2007; Maina et al., 2008; van Hooidonk and Hubert, 2009). Nevertheless, correlations between thermal stress indices and bleaching observations were high during the 1998 and 2002 largest events on record. Absence of bleaching in areas of observed thermal stress are noteworthy, as they may point to local scale hydrodynamic processes that efficiently mix water masses or to local ecological–biological adaptation to thermal stresses (Schiller et al., 2009).

### **Past and current application of ocean color passive sensors for indirect reef remote sensing**

Since 1978, ocean color sensors, like CZCS (Coastal Zone Coastal Scanner), SeaWiFS (Sea-viewing Wide Field-of-View Sensor, launched by the private company Orbimage), MODIS (Moderate Resolution Imaging Spectroradiometer), and MERIS (Medium Resolution Imaging Spectrometer) are typically multispectral with narrow bands, high sensitivity, and hectometric to kilometric spatial resolution sensors. These sensors were designed to measure chlorophyll concentrations in oceanic waters as a tracer of phytoplankton dynamics and primary productivity (Muller-Karger et al., 2005). The sensor's specifications have greatly improved through time to be able to accurately correct for the dominant atmospheric signal above the deep and dark oceanic waters, to estimate chlorophyll and other pigment concentrations, and to provide a suite of ocean color and atmospheric products for offshore and coastal waters. New missions are planned in the future by several space agencies, including using geostationary platforms (IOCCG, 1998, 1999; McClain, 2009).

Offshore, water color is dominated by phytoplankton and its residue. Along the coast, colored dissolved organic matter (CDOM, also called gelbstoff or yellow substances)



**Remote Sensing, Figure 4** Degree Heating Weeks in the Pacific Ocean in early 2002 at the beginning of a severe bleaching event (see Berkelmans et al., 2004). In the tropics, bleaching risks were detected as very high in eastern Australia, along the Great Barrier Reef. (Data courtesy of [http://coralreefwatch.noaa.gov/satellite/current/products\\_dhw.html](http://coralreefwatch.noaa.gov/satellite/current/products_dhw.html).)

and other inorganic–organic particulate suspended matter add to the complexity of the optical system. Ocean color sensors and processing methods have been primarily designed to monitor the dynamics of chlorophyll in the deep ocean. Coastal waters require specific algorithms accounting for the three components as well as the bottom signals in optically shallow water. These algorithms are now often locally optimized using in situ data and statistical and computer intelligence methods (IOCCG, 2000).

Waters circulating around reefs may import to remote reefs various dissolved and particulate material, from rivers and land. Conversely, reefs export material to the coast, deep ocean areas, and other reefs. Thus, ocean color data have been used to reveal the movement of water (physical connectivity) between land and reefs in the Caribbean and in Australia (Hallock et al., 1993; Gabric et al., 1990; Soto et al., 2009) to estimate the export of sediment after the passage of hurricanes in Bermuda and Cuba (Acker et al., 2004), and the export of CDOM from shallow seagrass-rich Bahamas bank areas to deeper water (Otis et al., 2004). Ocean color data are also used in large coastal systems like the Great Barrier Reef and the Florida Keys to routinely monitor water quality. These products are useful to examine the large-scale mechanisms that affect coral reefs, such as the influence of distant river mouths and their plumes, and algal blooms (Hu et al., 2004).

## Conclusions

Perhaps the main issues in reef remote sensing are related to the dispersal and transmission of knowledge and

expertise, so that images and products can be widely used. Despite the vast potential, and the fact that recent publications present applied remote sensing results set in an interdisciplinary framework, reef remote sensing mostly remains in the scientific and academic realm. It is far from having achieved its full potential for applied science, management, economic development, and capacity building.

Both producers and users need to examine the possibilities. Users should not be overwhelmed by the high-tech image that remote sensing carries and they should not have unrealistic expectations. It is possible to have excellent cost-effective reef-scale map products with simple processing of commercial high-resolution imagery, by favoring statistical and expert-knowledge-based approaches instead of more specialized physics-based approach. To monitor reef environments, managers can easily access indirect remote sensing products on public online servers, avoiding the need to process raw data themselves. On the other hand, remote sensing specialists should also be more attentive to the needs of managers and thematians. They should present to potential users the different panel of options, considering cost-effectiveness and the goals of the applications.

Technically, direct reef remote sensing will reach its full potential when affordable hyperspectral (or optimized multispectral) data is available on demand for any area worldwide, most likely through commercial channels. There is no doubt that hyperspectral images will significantly enhance the accuracy and thematic complexity of reef-scale mapping products. New fields of investigation will be opened. Hyperspectral data are also more suitable to physics-based approaches, and divergences between



different processing schools of thought may disappear. However, the handling and processing of these data may be less easily grasped by managers and nonspecialists. Thus, availability of hyperspectral data may not necessarily imply more products actively used for real-life reef environmental management.

Indirect remote sensing is a major topic, especially considering global climate change and its effects on coral reefs. Combined with modeling tools and computational approaches, it is expected that the indirect remote sensing will develop along three avenues: (1) integration of a wide panel of remotely sensed environmental products in addition to SST, solar insolation, cloud cover, and ocean color products (see Maina et al., 2008). Other applications related to climate change include monitoring swell and wind regime products from microwave scatterometer and altimeter instruments that have been seldom used in a coral reef context. Sea level variation is another key parameter to watch in a changing climate era; (2) multi-source data fusion will be enhanced by the use of in situ data and by the combined use of numerical circulation models, possibly through assimilation; and (3) local optimization will be favored, in order to replace global average products by fine tuned high-resolution (1–4 km) products that monitor the local processes more accurately (Maynard et al., 2008).

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## Cross-references

[Aerial Photography of Coral Reefs](#)  
[AUVs \(ROVs\)](#)  
[Climate Change and Coral Reefs](#)  
[Florida Keys](#)  
[Geomorphic Zonation](#)  
[Patch Reefs: Lidar Morphometric Analysis](#)  
[Reef Topographic Complexity](#)  
[Reef Structure](#)  
[Sediment Dynamics](#)  
[Seismic Reflection](#)  
[Seismic Refraction](#)  
[Swathe Mapping](#)  
[Turbid-Zone and Terrigenous Sediment-Influenced Reefs](#)  
[Underwater Landscape Mosaics](#)

## RESIDENCE TIME

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### Synonyms

Flushing time; Mixing time; Water age

### Definition

The residence time is the characteristic time that a parcel of water will remain within a water body. The quantitative definition of “residence time” varies in the literature (Monsen et al., 2002). Generally, it is implied that a complete exchange of the water does not occur in this time. For this reason, the residence time is sometimes defined as the time for some fraction of the water to be exchanged.

The residence time in a partially enclosed water body varies with oceanographic conditions, such as tides, waves and oceanic currents, and depends on the size of the water body and the degree of hydrodynamic connection with adjacent water bodies. Residence time is one of the key parameters controlling the fate of solutes in an enclosed water body such as a coral reef lagoon. A long residence time could, for example, allow accumulation of pollutants. Residence time can also be very important in the (passive) dispersal of larvae.

The residence time can be calculated by hydrodynamic modeling, using virtual lagrangian drifters. For direct measurement in small systems, a dye can be artificially injected and its movements followed, and in larger systems naturally occurring tracers such as the concentration of salt or radionuclides are used.

Tracer data in the central Great Barrier Reef lagoon indicate typical residence time scales of weeks, ranging between 2.5 and 6.5 weeks from inner to mid shelf and from mid shelf to outer shelf respectively (e.g., Hancock et al., 2006). In contrast, residence times inferred from a numerical model of the same region are around six months (Luick et al., 2007), indicating a need for ongoing research to resolve such discrepancies between measured and modeled results.

On spatial scales of coral atolls or single reefs, residence time can vary widely depending on driving forces from a few hours in a small coral reef to tens of days in larger reefal lagoons (Kraines et al., 1998; Delesalle and Sournia, 1992).

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### Cross-references

[Great Barrier Reef Committee](#)  
[Heavy Metal Accumulation in Scleractinian Corals](#)  
[Lagoon Circulation](#)  
[Nutrient Pollution/Eutrophication](#)

## RETICULATED REEFS

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### Definition

Reticulated, or reticulate, reefs are networks of linear or polygonal reef framework with intervening depressions (the larger of which are called blue holes), which may occur on fringing reefs, barrier reefs, and atolls.

### Introduction

Networks of linear or polygonal reef framework, forming a honeycomb-like mesh of coral-fringed depressions are known as reticulated or reticulate reefs. They occur on fringing reefs (e.g., Red Sea, Shroeder and Nasr, 1983; Madagascar, Guilcher, 1988), barrier reefs (e.g., New Georgia, Stoddart, 1969; Belize, Purdy, 1974; the Great Barrier Reef, Marshall and Davies, 1982; Hopley et al., 2007; Mayotte, Guilcher, 1988; Society Islands, Guilcher, 1988), and on atolls, where they are so distinctive that Guilcher (1988) recognized “reticulated atolls” as a distinct atoll morphology.

Mataiva, the most northwesterly of all the Tuamotu atolls, is a relatively small atoll (10 km by 5 km), but its lagoon with an area of 25 km<sup>2</sup> comprises a particularly distinctive network of reticulated reefs (Figure 1). The reefs, ranging in width from 30 to 300 m, divide the lagoon waters into a series of shallow depressions (Delesalle, 1985; Adjias et al., 1990). Mataiva has an almost continuous reef island around its perimeter, and small reef islands are also found on the reticulated reefs themselves.

Reticulate reefs are apparent in many atoll lagoons (Shepard, 1970). Kanton, known as Abarringa, the most northerly of the Rawaki Islands in the Phoenix group of central Kiribati also has a prominent reticulated lagoon, as does Fanning Atoll in the Line Islands. Many of the northwestern Hawaiian Islands show a reticulate pattern





**Reticulated Reefs, Figure 1** An oblique aerial view of Mataiva, the northwesternmost of the Tuamotu atolls, which has a particularly well-developed network of reticulated reefs in its lagoon.

of reefs, most prominent on Pearl and Hermes, Lisianski Island, Maro, and French Frigate Shoals (Rooney et al., 2008). Similar reticulate patterns occur in the lagoons of other atolls in both the Pacific Ocean (e.g., Eniwetok and Bikini, Emery et al., 1954; Elizabeth Reef at the southern limit to reef development in the Pacific, Woodroffe et al., 2004) and Indian Ocean (e.g., the Cocos (Keeling) Islands, Woodroffe et al., 1994).

On Christmas Island (Kiritimati), the largest of the atolls in the Line Islands of eastern Kiribati, the reticulate pattern of reefs is largely emergent above sea level. The lagoon has a complex pattern of shallow coral patches and sand bars, and this pattern grades to the east into a barren scrub-covered hardpan covering the island's interior. Within this there is a maze of hypersaline pools separated by emergent fossil reefs of mid-Holocene age (Woodroffe and McLean, 1998).

Reticulated reefs are also found in other reef systems. In the Caribbean, they occur at Alacranes on the Mexican coast and in Golfo de Guacanayabo in Cuba. There are reticulate reefs within the barrier reefs of New Caledonia, such as at Tétambia Reef. They are also apparent on the eastern margin of the reef platforms of the Abrolhos Islands in Western Australia.

### Mode of formation of reticulate reefs

The most widely held view is that reticulated reefs develop through a combination of vertical reef growth, forming the reef framework, and subaerial solution by processes of karstification at times of lower sea level, which

accentuates the depressions between the reefs (Guilcher, 1988). The important role that erosional processes play during times of lower sea level, and the subsequent drowning of this antecedent topography, with reef establishment over the topographic high points has been widely recognized (MacNeil, 1954; Purdy, 1974; Hopley et al., 2007). Mildly acidic rainfall results in gradual dissolution of limestone generating a pitted topography of enclosed depressions bounded by steep margins (Solution processes/Reef erosion). The deeper depressions are called blue holes (*Blue Hole*). This view seems to explain many of the features of reticulated reefs, but is not universally accepted (e.g., Gray, 1991; Purdy and Winterer, 2001).

In the case of Mataiva, the distinct nature of the lagoon has been attributed to an earlier phase of erosion of a dolomitized and phosphatized pre-Pleistocene limestone surface that is exposed around the atoll rim (Delesalle, 1985). Emergence during the mid- or late Holocene has resulted in some of the reticulate reefs of the Mataiva lagoon becoming exposed above sea level which has enabled islands to form on them. The interior of Christmas Island, described above, with its maze of hypersaline lakes appears to represent a further stage in this process of emergence.

An alternative view has been proposed for the origin of the network of blue holes in the Abrolhos Islands by Wyrwoll et al. (2006), based on drilling and dating. Their studies have shown thicknesses of more than 20 m of Holocene reef growth and they view the reef framework as constructional rather than the product of karst erosion at lower sea level.

Extensive karst erosion also seems unlikely in very arid areas, but in many places, such as the Red Sea, there are prominent reticulate reefs. Purkis et al. (2010) have recently suggested that the network of reefs indicates solution of limestone foundations beneath these reefs and is evidence for altered climate in this region over the late Quaternary, particularly a wetter phase a few thousand years ago.

## Summary

Networks of reticulated reefs show similar mesh-like morphology on reefs from around the world. Whereas subaerial karst erosion during times of lower sea level seems to have contributed to the development of most of these patterns, there are situations where other factors may have played a role in their formation. Constructional reef growth is important in their development, isolating the intervening depressions which are then unable to support coral growth.

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## Cross-references

[Antecedent Platforms](#)  
[Atolls](#)  
[Blue Hole](#)  
[Cocos \(Keeling\) Islands](#)  
[Lagoons](#)  
[Solution Processes/Reef Erosion](#)  
[Western Australian Reefs](#)

## RHODOLITHS

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## Synonyms

Red algal nodules (balls or macroids); Rhodoids

## Definition

Rhodoliths are defined as free-living nodules that are dominantly composed of calcifying red algae (mostly corallinaceae, occasionally peyssonneliaceae) commonly associated with other encrusters (foraminifera, bryozoans, bivalves, serpulid worms and/or corals). Their size ranges from less than 30 mm to about 300 mm (Bosellini and Ginsburg, 1971).

*Habitat and biotic composition:* Rhodolith deposits occur worldwide along shelves at euphotic depths (generally less than 150 m). The shape, internal structure, composition and growth rate of rhodoliths vary according to environment, water energy and depth. In reef provinces, the nodules from shallower, high to moderate energy environments (e.g., reef flats, proximal back-reefs and channels) exhibit massive spheroidal to branching ellipsoidal types, made up of mastophoroid (*Hydrolithon*, *Neogoniolithon*) and/or lithophylloid (*Lithophyllum*,

*Dermatolithon*, *Titanoderma*) laminar crusts growing over a core. Locally, at distal backreef to lagoonal settings, rhodoliths can be monospecific resulting from the isotropic accretion of a single thallus. Those from deeper (greater than 10 m) and low-water energy (e.g., fore-reef slopes and terraces) preferentially form massive to branching, ellipsoidal to discoidal growths composed of melobesioids (*Mesophyllum*, *Lithothamnion*) and lithophylloids, together with occasional mastophoroids and sporolithaceans. The accretionary rates of shallow-water nodules range from about 0.15 to up to 2 mm year<sup>-1</sup> (Bosence, 1983) while those of fore-reef zones are substantially lower, from 0.010 to 0.40 mm year<sup>-1</sup> (Reid and Macintyre, 1988).

**Environmental significance:** Spheroidal growths are considered to be maintained by periodic movement by waves and currents; with increasing size, movement becomes less frequent. Ellipsoidal and discoidal still move around. The attributes of rhodoliths are therefore used as paleoenvironmental indicators, although in many cases these are not sufficiently significant in terms of ecological conditions (Reid and Macintyre, 1988).

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## Cross-references

Algae, Coralline  
Ecomorphology  
Lagoon Circulation  
Reef Flats  
Waves and Wave-Driven Currents

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## RIVER PLUMES AND CORAL REEFS

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## Definitions

River plume: a discrete body of fresh or low-salinity water discharged from a river mouth into coastal waters.  
Coriolis force: the deflecting effect of the earth's rotation on a moving fluid.

## Introduction

A significant proportion of coral reefs are located close to continental or high-island land masses where they are influenced by terrestrial runoff (Furnas, 2003). This runoff may come from larger rivers or small coastal streams which inundate reefs near the stream mouth. The frequency and intensity of runoff affecting reefs depends on local or regional rainfall distributions, intensity, and duration, which determine the volume and timing of runoff. Coral reefs are widely distributed in parts of the world influenced by monsoonal climate regimes, where there is often a pronounced wet season.

Runoff affects coral reefs in a variety of ways. These include the direct osmotic stress of low salinity on corals (van Woesik and Done, 1997), the influence of suspended sediment (blanketing after deposition, shading; Philipp and Fabricius, 2003), nutrient enrichment of coastal waters (Furnas, 2003), and the transport of terrestrial pollutants into coastal ecosystems (Shaw and Mueller, 2005).

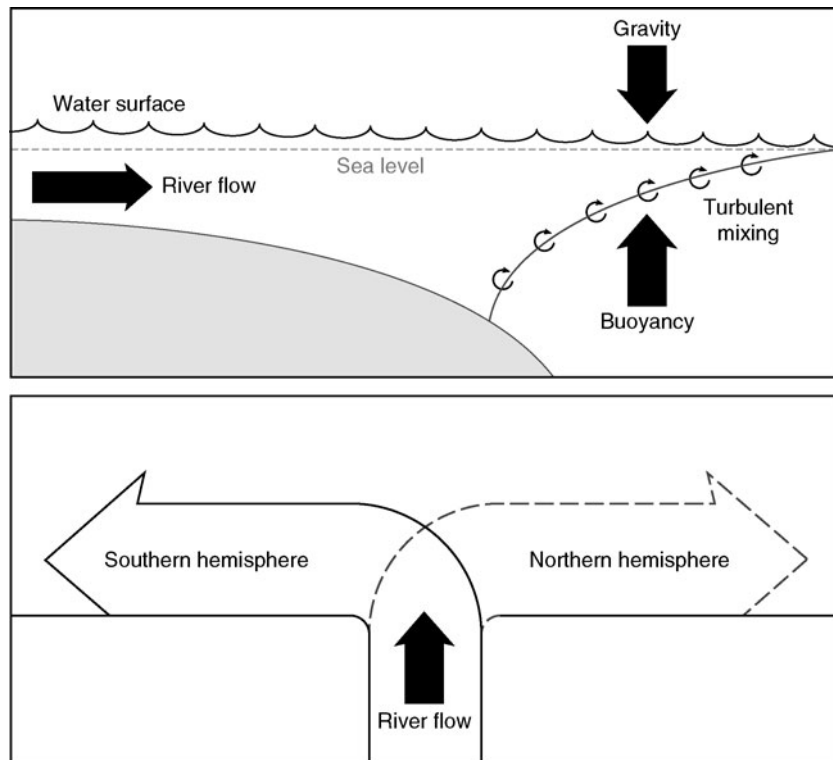
While there is much attention given to the negative effects of runoff on corals and coastal reefs, it is important to remember that coastal reefs often develop in locations with persistent or episodic influence by runoff from natural sources. The location and extent of these reefs reflect long-term interactions between reef growth, disturbance, and mortality due to runoff effects. Nutrients and organic matter in runoff support the wider productivity of coastal ecosystems which sustain corals, plants, and animals living in coastal reefs. Modern changes in coastal and nearshore coral reefs influenced by runoff are largely due to changes in the quantity and nature of materials carried in runoff due to human numbers and land use in catchments rather than changes in the volume of freshwater.

## Formation of River Plumes

In many tropical systems, most freshwater runoff occurs during short-lived episodic or seasonal flood events. During floods, freshwater is pushed through the estuary of coastal rivers and streams, and freshwater plumes extend into coastal waters where fresh and salt waters mix. Freshwater (ca. <1 g dissolved salts L<sup>-1</sup>,  $\rho \approx 1.0 \text{ g cm}^{-3}$ ) has a lower specific gravity (density) than saltwater (33–35 g dissolved salts L<sup>-1</sup>,  $\rho \geq 1.02 \text{ g cm}^{-3}$ ) and floats on top of seawater. Mixing between the fresh and salt water is determined by the amount of physical energy in the system (turbulence) and the density difference between the two water types. The surface layer of freshwater in a river plume may range in thickness from many meters to a few centimeters. It is affected by a number of forcing processes, including wind stress, gravity, and the Coriolis force.

Water coming from a river or stream mouth does not spread uniformly across the surface of adjacent coastal





**River Plumes and Coral Reefs, Figure 1** *Top:* Schematic section through a river plume showing the buoyant plume and the wedge of freshwater in relation to normal sea level. *Bottom:* Schematic diagram of the effect of Coriolis force on river plumes in the Northern and Southern Hemisphere.

waters. The discharged water forms a shallow wedge near the stream mouth (Figure 1). As gravity and buoyancy flatten this wedge, the water is accelerated away from the coast. The moving water comes under the influence of the Coriolis force and is deflected to the right (Northern Hemisphere) or left (Southern Hemisphere). In the absence of currents or other stresses, this causes the flowing plume of river water to turn parallel to the coast, forming a coast-hugging buoyancy current (Burrage et al., 2003). The plume then flattens and disperses due to horizontal and vertical turbulence as it moves along the coast. Plumes from small streams may only go a small distance before dispersing. In contrast, plumes formed by larger rivers such as the flooding Burdekin River in the Great Barrier Reef (Figure 2) may extend for > 500 km along the coast (Wolanski and van Senden, 1983; King et al., 2002).

### Materials in River Plumes

Rivers carry a large variety of dissolved and particulate materials into the sea. The most obvious is the suspended sediment. During flood events, in particular, rivers and streams can be highly turbid with suspended loads reaching several grams per liter. Tropical rivers may also

contain substantial amounts of dissolved and particulate organic matter from eroded soils. The dissolved organic matter (DOM) may be highly colored (colored or chromophoric dissolved organic matter – CDOM), which affects the optical properties of river plumes.

Most suspended sediment carried by rivers is deposited close to the river mouth as flow slows and the turbulent energy of the stream dissipates in the ocean. The mixing of fresh and salt waters causes fine sediment particles and organic macromolecules in the river water to aggregate into larger particles or flocs which rapidly sediment from the water column. Reefs located near river or stream mouths can receive significant sediment loads during flood events, with the sediment blanketing reef surfaces and causing reductions in underwater light levels. The formation of coastal boundary currents tends to trap terrestrial materials in the nearshore zone (e.g., Currie and Johns, 1988; Gagan et al., 1987).

Concentrations of individual forms of dissolved matter can exhibit both conservative and nonconservative behavior in river plumes as fresh and seawater mix. Conservative behavior indicates that concentration changes follow a linear relationship with salinity (Figure 3). Dilution is the governing process.



**River Plumes and Coral Reefs, Figure 2** Natural color satellite imagery of river plumes entering the central Great Barrier Reef (17–19°S) following heavy rainfall in adjacent catchments, February 2007. The large plume at the *bottom* is from the Burdekin River. Data source: NASA GSFC. Processed by M. Slivkoff, AIMS.

Nonconservative behavior is characterized by nonlinear relationships between concentration and salinity. It occurs when ions dissociate or desorb from dissolved or particulate matter as fresh and saltwater mix, or are removed due to precipitation, adsorption onto particles, or biological uptake.

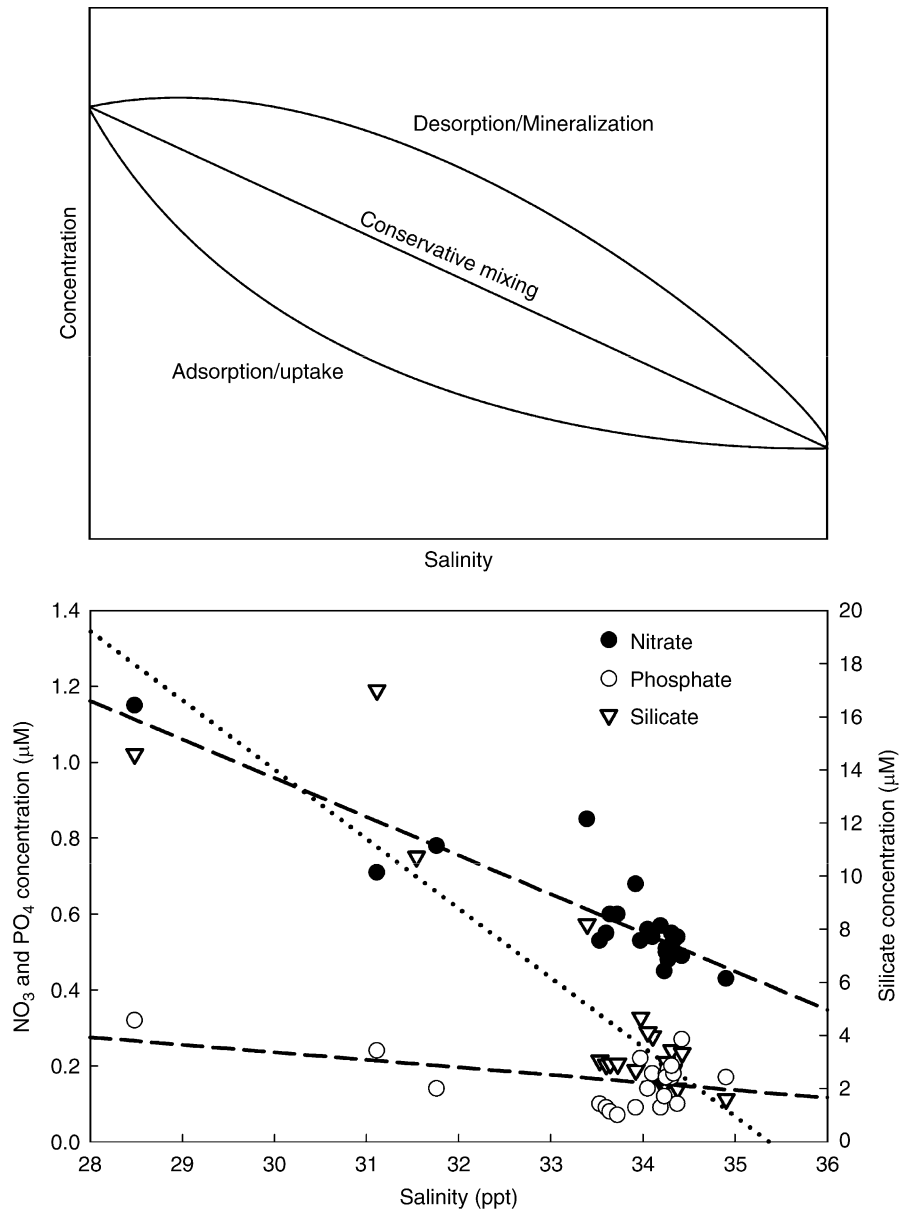
Dissolved nutrients ( $\text{NO}_3^-$ ,  $\text{PO}_4^{3-}$ ,  $\text{Si(OH)}_4$ ) typically exhibit conservative behavior in the early phases of river plume development as fresh and seawater mix but before there has been sufficient time for significant phytoplankton growth (e.g., Devlin and Brodie, 2005). Once significant phytoplankton growth gets underway in the plume waters (Furnas, 1989), nutrient concentrations can be rapidly reduced through uptake, and concentrations exhibit nonconservative salinity distributions. Iron ( $\text{Fe}^{2+}$ ) typically exhibits strong nonconservative behavior in river plumes, as ferric iron is highly insoluble in oxic seawater.

Dissolved nutrient concentrations in river waters are typically many times higher than those occurring in coastal coral reef waters (e.g., Devlin and Brodie, 2005). These nutrients frequently lead to the development of phytoplankton blooms in plume waters. Phytoplanktons, in turn, produce much of the organic matter which supports coastal food webs of pelagic and benthic filter feeders accessible to reef organisms. A small portion of the nutrients may be taken up directly by reef algae and stimulate growth on the reef surface. While high nutrient concentrations may be detrimental to corals and other reef organisms, the direct effect of nutrients in river plumes is less pronounced than the effect of the lower salinity in the plume. Exposure times are usually brief. Most river-derived nutrients are delivered to reefs in the form of dissolved and particulate organic matter which has been taken up by phytoplankton and bacteria and cycled through coastal food webs.

Rivers flowing through agricultural lands also transport a range of agricultural chemicals (Shaw and Mueller, 2005). Elevated concentrations of herbicides and pesticides have been measured in river plumes discharged into the Great Barrier Reef, for example (Lewis et al., 2009). Herbicides, in particular, can exert a detrimental effect on corals. Direct effects of agricultural chemicals on reef systems are not well characterized at this time, particularly in synergy with other stresses associated with river plumes (low salinity).

### Summary

Flooding rivers and streams often form buoyant plumes of fresh and low-salinity water in adjacent coastal zones. In the absence of contrary wind stress, the Coriolis force constrains plumes to a coastal band. Corals and coral reefs can grow in runoff-affected coastal areas when the frequency and intensity of disturbance by freshwater and sediments are low enough to allow ongoing (re-) growth after disturbance events. Nutrients in runoff contribute to the overall productivity of the coastal zone, but can stimulate



**River Plumes and Coral Reefs, Figure 3** Top: Schematic depiction of conservative and nonconservative behaviors of dissolved materials in river plumes. Bottom: Relationships between the concentrations of nitrate, phosphate, silicate, and salinity in the plume of the Tully River after cyclone Winifred, February, 1986 (M. Furnas, unpublished data).

phytoplankton blooms or enhanced growth of benthic algae which can compete with corals. Levels of sediment, nutrients, and other pollutants have increased in modern runoff due to more intensive and extensive human land use in catchments, which may be detrimental to corals in coastal systems.

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## Cross-references

[Impacts of Sediment on Coral Reefs](#)  
[Nutrient Pollution/Eutrophication](#)  
[Turbid-Zone and Terrigenous Sediment-Influenced Reefs](#)

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## ROYAL SOCIETY OF LONDON

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### Definition

The Royal Society of London is a learned society for science, founded in 1660, which serves as the Academy of Sciences of the U.K.; membership (Fellow of the Royal Society) is a great honor. It funds, publishes, and publicizes scientific research and advises the U.K. Government.

### Background and roles

The Royal Society of London for the Improvement of Natural Knowledge, known simply as the Royal Society, or even the Royal, is a learned society for science. Founded in 1660, it is generally considered to be the oldest such society still in existence. A charitable body whose patron is the reigning monarch, it serves as the Academy of Sciences of the United Kingdom (in which role it receives funding from the U.K. Government). Fellowship (FRS), granted for life, is awarded to scientists after their election by existing Fellows, and is considered a great honour. Fellows must be citizens or residents of a member of the Commonwealth of Nations or the

Republic of Ireland, while a smaller number of Foreign Members (ForMemRS) are drawn from other countries. Fellows from coral reef science in the nineteenth and twentieth centuries have included C.R. Darwin (elected FRS 1839), J.B. Jukes (1853), W.J. Sollas (1889), T.W. Edgeworth David (1900), J. Stanley Gardiner (1908), H.B. Guppy (1918), R.B. Seymour Sewell (1934), and C.M. Yonge (1946). J.D. Dana (1884) and Alexander Agassiz (1891) were elected as Foreign Members. Both Darwin and Dana were holders of the Society's oldest medal, the Copley Medal, and Gardiner and Yonge were awarded the Darwin Medal for their coral reef research. The Society provides reports and science policy advice to the U.K. Government (as for example in the 2005 Report on ocean acidification), promotes the public understanding of science, runs programs to encourage international collaboration in research, and publishes a number of serial titles, including the world's longest running scientific journal (continuously since 1665), the *Philosophical Transactions of the Royal Society*. However, its prime role is to support fundamental research, and in that regard the Society has been intimately involved for over 300 years in promoting and financing coral reef research (Yonge, 1980; Fogg, 2001).

### Support of exploration of the reef seas

From the beginning, the Society wished to expand knowledge of the world's oceans, issuing "Directions to seamen bound for far voyages" in the first volume of the *Transactions* with the aim of gathering observations of scientific value. This was a challenge taken up, by example, by Edmond Halley (FRS 1678) in his late seventeenth century observations on trade winds, ocean currents, and geomagnetic variations in the Atlantic Ocean (Cook, 1998) and by William Dampier who dedicated "A new voyage around the world" (1697) to the then President of the Society, Charles Montague, Earl of Halifax (Preston and Preston, 2004). It was the Society's Transit Committee that recommended that the 1769 transit of Venus across the face of the sun (to aid the determination of true distances in the solar system) should be observed from a site in the South Seas, leading directly to Captain James Cook's (FRS and Copley medallist 1776) first voyage (1768–1771) to Tahiti. From Tahiti, the expedition undertook the first mapping of the Great Barrier Reef, including the disastrous encounter with the Reef at what is now Endeavor Reef on June 11, 1769. The collections made by Joseph Banks (FRS 1776; President of the Royal Society 1778–1820) and Daniel Solander (FRS 1764) included corals; these were described in *The natural history of many curious and uncommon zoophytes collected from various parts of the globe*, authored by John Ellis (FRS 1754; Copley medallist 1767 and an early proponent of reef-building corals being animals) and Solander and published in 1786. Cook's second voyage (1772–1775), sponsored by the Society to search for the mythical "Terra Australis", utilized the Larcum Kendall K1 chronometer

(a copy of John Harrison's clock H4), which enabled Cook to calculate his longitudinal position with much greater accuracy and thus marked a step change in the positioning of islands within the reef seas. It was the naturalist Johann Reinhold Forster (FRS 1772) on this voyage who made the fundamental distinction between "high" islands, thought to be the product of earthquakes and volcanic activity, and "low" islands, formed by sinking and coral growth (Hoare, 1982). In the nineteenth century, through its Circumnavigation Committee, the Society obtained the use of *HMS Challenger* from the Royal Navy and in 1872 modified it for scientific work, equipping it with separate laboratories for natural history and chemistry. Under the scientific supervision of Charles Wyville Thomson, the voyage (1873–1876) effectively marked the birth of modern oceanography, covering over 100,000 km and conducting almost 500 deep-sea soundings, over 100 bottom dredges and open water trawls, and over 250 measurements of water temperature; the Expedition Report catalogued over 4,000 previously unknown species (Deacon, 1971). The Society was instrumental in attempting to test Darwin's subsidence theory by supporting three expeditions to Funafuti, Ellice Islands (now Tuvalu; see *Funafuti Atoll*), between 1896 and 1898, albeit inconclusively (Royal Society, 1904; Spencer et al., 2008). In the early twentieth century, the Society provided financial support for the 1928–1929 Great Barrier Reef Expedition, which set new standards for field-based coral reef physiology, ecology, and geomorphology; in addition to its leader, C.M. Yonge, four other expedition members became Fellows of the Society (F.S. Russell (1938), S. Manton (1948), T.A. Stephenson (1951), and S. Marshall

(1963)). From 1956 onwards, The Society has supported coral reef research through what since 1964 has been known as the Southern Zone Research Committee. The Committee organized the 1965 expedition to the British Solomon Islands Protectorate (leader: E.J.H. Corner (FRS 1955)); jointly with the Royal Society of New Zealand, the 1969 Cook Bicentenary Expedition to Tonga and the Southern Cook Islands (Stoddart and Gibbs, 1975); and the 1971 Royal Society–Percy Sladen expedition to the New Hebrides. In 1973, jointly with the Universities of Queensland, Australia, the Society organized a largely geomorphological expedition to the northern Great Barrier Reef (leader: D.R. Stoddart), in part revisiting the field sites of the 1928–1929 expedition (Figure 1).

Since the 1960s at a smaller scale, funds from the Society have also been used, *inter alia*, to support reef research in the Maldives (at Addu Atoll), Amirantes and southern Seychelles, and Diego Garcia in the Indian Ocean; and in the Phoenix Islands, Austral Islands, and Northern Cook Islands in the Pacific Ocean. In 1966–1967, the Royal Society was centrally involved in opposing U.K. Government plans to build a military base on the relatively undisturbed raised limestone island (and now World Heritage Site) of Aldabra Atoll in the south West Indian Ocean. Following an initial ecological inventory and expeditionary phase between 1966 and 1969, the Society built and administered the Aldabra Research Station between 1971 and 1979 before handing over its responsibilities to an independent trust, the Seychelles Island Foundation. It has been estimated that the Society supported the equivalent of over 50 person-years of research effort into physical and ecological monitoring



**Royal Society of London, Figure 1** Members of the 1973 Great Barrier Reef Expedition outside the Royal Society's rooms at Carlton House Terrace, London, prior to the Discussion Meeting of 28–29 January 1976. From *left to right*: D.Hopley; P.E.Gibbs; R.F. McLean; G.R.Orme; D.R.Stoddart (expedition leader); P.G. Flood; †T.P.Scoffin; and B.G. Thom (photograph: P.G. Flood).

and experimentation at Aldabra, making it probably the most intensively studied atoll ecosystem in the world (Westoll and Stoddart, 1971). Finally, between 1998 and 2001, the Society, through its Environmental Research Programmes and in partnership with the Royal Geographical Society of London, supported the Shoals of Capricorn Marine Research Programme in the western Indian Ocean (Spencer et al., 2005).

## Summary

From its earliest beginnings in the seventeenth century, the Royal Society of London has promoted the interdisciplinary exploration of the reef seas, particularly in the Southern Hemisphere. The Society, both as a body and through the individual research activities of its Fellows, has made major contributions to the study of physical and geological oceanography; the establishment of the tectonic histories of coral reefs, both in the mid-ocean basins and on their margins; and the understanding of the biogeography and ecology of coral reefs.

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## Cross-references

- Agassiz, Alexander (1835–1910)
- Cook, James (1728–1779)
- Dana, James Dwight (1813–1895)
- Darwin, Charles (1809–1882)
- David, Tannant Edgeworth (1858–1934)
- Gardiner, John Stanley (1872–1946)
- Ocean Acidification, Effects on Calcification
- Steers, James Alfred (1899–1987)
- Stoddart, David Ross (1937–)
- Subsidence Hypothesis of Reef Development
- Yonge, Sir Maurice (1899–1986)

## RUDSTONE

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Rudstone is a type of limestone that displays 10% or more of the grains larger than 2 mm in diameter, and there is spar between the grains (like grainstone–sand-sized).

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## Cross-references

Porosity Variability In Limestone Sequences

## RYUKYU ISLANDS

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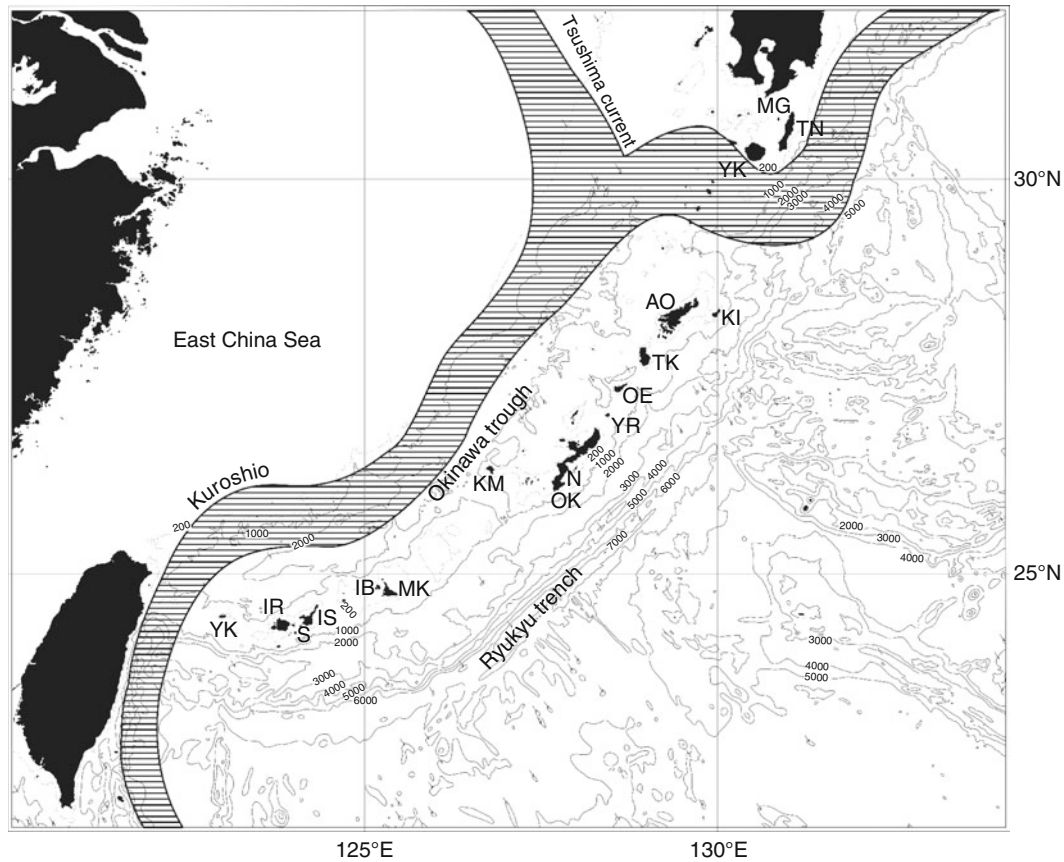
## Synonyms

Nansei Shoto (Islands); Ryukyus

## Introduction

Ryukyu Islands located in the northwestern Pacific at South Japan, latitudes between 24° and 30°50'N, longitudes between 123° and 131°E (Figure 1). The coral reefs





**Ryukyu Islands, Figure 1** Topographic map of the Ryukyus. Hatched line indicate the major route of Kuroshio Current and a branch current of Tsushima Current based on the sea surface current at 50 m depth line for November 2009 calculated by Japan Meteorological Agency. YK: Yonakuni Island, IR: Iriomote Island, IS: Ishigaki Island, S: Sekisei Reef, MK: Miyako Island, IB: Irabu Island, KM: Kume Island, OK: Okinawa Island, N: Nakagusuku Bay, YN: Yoron Island, OE: Okierabu (Okinoerabu) Island, TK: Tokunoshima Island, AO: Amami Oshima Island, KI: Kikai Island, YK: Yaku Island, TN: Tane Island, and MG: Mage Island. Depth in meters.

develop at high latitude because of the major western boundary current, Kuroshio Current flows through the Ryukyu Islands. The Kuroshio Current originates from the Western Pacific Warm Pool (WPWP) and flows through a part of “coral triangle,” the major marine biodiversity center in the Southeast Asia. Consequently, Ryukyu Islands are one of the richest multitaxon centers of endemism in the world’s coral reefs (Roberts et al., 2002).

### Geological setting

The Ryukyu Islands form an island arc parallel to the Ryukyu trench where the Philippine Sea plate subducts into the Eurasia Plate. Initial rifting of the back-arc basin Okinawa Trough occurs around 10 Ma after a major early Miocene change in the motion of the Philippine Sea plate (Sibuet et al., 1987; Furukawa, 1991). It ceased briefly during the Pliocene at 4 Ma, with a second rifting phase starting at about 2 Ma. Coral reef formation in Ryukyu Island started at the early Pleistocene (Yamamoto et al.,

2006) unconformably on the Tertiary Shimajiri Group, consisting mainly of siliciclastic siltstone.

At islands subjected to uplifting in the active margin, the reefs in the different time series are not overlapped and reef terraces are developed. Therefore, the major reef type in the Ryukyu Islands is fringing reef, with the exception of three barrier reefs due to local tectonic subsiding: the Sekisei Reef, 30 km × 20 km reef located between Ishigaki and Iriomote Islands; the Nakagusuku Bay, 20 km × 20 km reef located southeastern Okinawa Island; and the eastern Kume Island, 13 km × 6 km reef. The Holocene uplifted reefs have also developed in some islands subjected to active uplifting such as Kikai, Kume, Takara, and Kodakara Islands (e.g., Koba et al., 1979; Takahashi and Koba, 1977; Sasaki et al., 1998; Ota et al., 2000; Sugihara et al., 2003).

### Climate conditions

The average (1971–2000) monthly maximum in (minimum) air temperatures, annual rainfall, and average

monthly maximum (minimum) sea surface temperatures (SST) of the Ishigaki Island in the Southern Ryukyus, the Naha in the Central Ryukyus and Tane Island in the Northern Ryukyus are 29.3°C (18.3°C) 2,060 mm SST 29°C (23°C), 28.5°C (16.6°C) 2,037 mm SST 28°C (21°C), 27.7°C (11.7°C) 2,330 mm SST 28°C (19°C), respectively (Japan Meteorological Agency, 2009). The large latitudinal gradient occurs at the minimum air and sea temperature in winter. The difference in minimum SST creates the latitudinal gradient in coral reef development in the Ryukyus (Hori 1980).

Prevailing wind directions in Ryukyu Islands are NW to NE in winter and S to SE in summer (Japan Meteorological Agency, 2009) influenced by East-Asian monsoon. The typical windward/leeward reefs as in the trade wind zone are not found in the Ryukyus and fringing reefs are surrounding the islands due to the reversal of the windward by seasons. The Ryukyu Islands are also located at the horse latitude in the typical track of typhoons originating from the WPWP. Typhoons develop to a maximum strength and reducing speed around the Ryukyus. Storm surge at typhoons plays an important role on reef-edge sediments and boulders on reef flats in Ryukyus along with tsunami surge (e.g., Kawana and Nakata, 1994; Kan, 1995; Onda, 1999; Suzuki et al., 2008; Goto et al., 2009).

### Start-up growth of the postglacial reefs

In the Ryukyu Islands, a reef developed in the last glacial period was discovered by drilling an island shelf off the Irabu Island (Sasaki et al., 2006). This reef grew from 22 to 15 ka at the present depth of 126.2–123.2 m and gave up its growth with the postglacial sea level rise.

The modern reefs developed along the present shorelines began to grow in the Holocene period. In the Southern Ryukyus, the start-up growth of modern reef occurred around 8000 BP ( $^{14}\text{C}$ ) on the extensive antecedent platform around 20 m at Sekisei Barrier Reef (Kan and Kawana, 2006). On the Ishigaki Island, where fringing reef of 1–1.5 km width surrounds the island, reef started to grow around 7400 BP ( $^{14}\text{C}$ ) from around 20 m deep (Hongo and Kayanne, 2009).

In the Central Ryukyus, the modern reef started to grow around 8000 BP ( $^{14}\text{C}$ ) from 17 m deep in the southeastern Okinawa Island (Kawana and Kan, 1996, 2002) and 7900 BP ( $^{14}\text{C}$ ) from 15 m deep in the Kume Island (Takahashi et al., 1988; Kan et al., 1991, 2000). In the Okierabu Island, reef started to grow at 7500 BP ( $^{14}\text{C}$ ) from 10 m deep (Kan et al., 1995). The early start-up growth of around 10 ka and formation of 25 m-thick reef limestone has been reported in the Kikai Island (Konishi et al., 1978, 1983; Webster et al., 1998; Sasaki et al., 1998), where active uplift of 1.8 m/ka took place at least in the late Pleistocene (Ota et al., 2000; Sasaki et al., 2004).

In the Northern Ryukyus, the recent drilling research shows the lagged start-up growth around 6100 BP ( $^{14}\text{C}$ )

in the Mage Island at latitude in 30°45'40"N, where the maximum thickness of the Holocene reef is 4 m (Kan et al., 2006).

### Development of Holocene reefs and their zonation

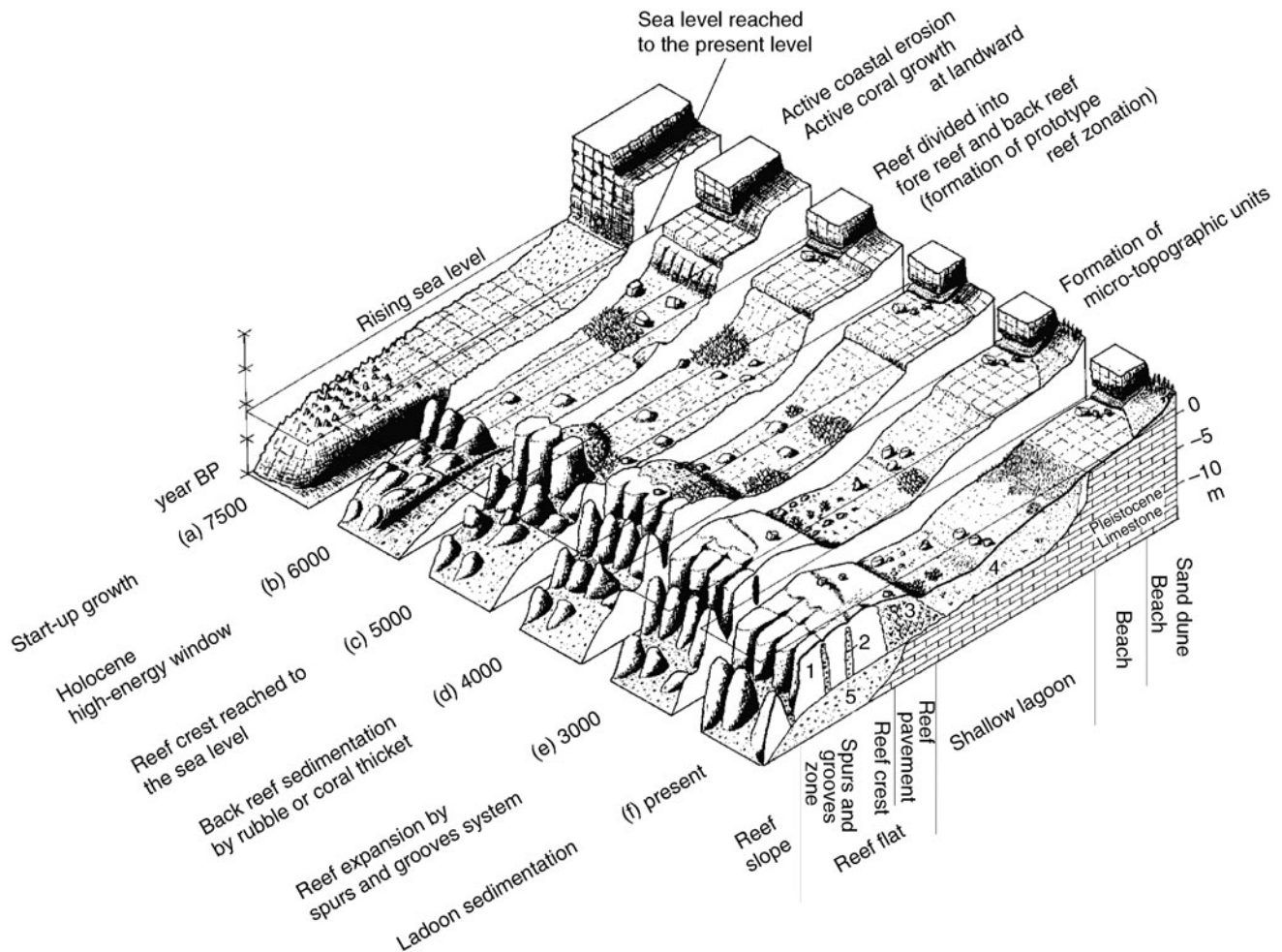
When the sea level reached its present position of about 6500 BP (Alley et al., 2005), the wave-resistant structure, such as the present reef edge, had not been formed before the reefs grew to reach sea level (Figure 2b). The initial reef growth to reach the sea level lags at least 500–1,000 years behind sea level rise. Before the reef first reached the sea level, the strong wave condition was assumed for coastal zone because of less wave attenuation in reef (i.e., “Holocene high-energy window”). This condition causes the active coastal erosion to form bench and cliff along the uplifted Pleistocene limestone coasts and also sometimes induces the active coral growth landward.

The timing of the reefs that have reached the sea level varies from 6100 BP to around 4000 BP ( $^{14}\text{C}$ ) in the Southern and Central Ryukyus with the average upward growth rate of around 4 m/kyr (e.g., Takahashi et al., 1988; Kan and Kawana, 2006) mainly by corymbose coral community (Hongo and Kayanne, 2010). The primary growth of the reefs usually with tabular corals acted as a breakwater and differentiated the reef into a fore-reef zone and a back-reef zone (Figure 2c). The reef first reached sea level forming the reef crest ridge of the present reef and is interpreted as the functional core for reef zonation.

After the crest growth, the back reef, especially seaward of the lagoon, was infilled by thickets of in situ ramose corals and accumulation of coral debris derived from the reef edge (Figure 2d). The vigorous back reef accumulation up to 10 m/kyr ends up about 500 to 1,000 years after the crest growth (Takahashi et al., 1988; Kan and Hori, 1993).

Simultaneously, the area of active reef growth has shifted progressively seaward with the development of reef edge spurs. The micro-topographic units along reef margins such as spurs, grooves, and reef tunnels are formed in this stage. The pinnacles in front of the established spur and groove system reach sea level and the reef margin migrate seaward (Figure 2e). This gradual process is called “reef flat accretion” (Kan and Hori, 1993) and has contributed to the build-up of expanded reef flat under almost stable sea level condition in the late Holocene.

The strong zonal patterns emerge when the energy-related gradient develops. In the middle Holocene, the reef first reached the sea level, which acted as a breakwater and differentiated the reef into a fore-reef and a back-reef. The fringing reef lagoon may have been formed by a damming process where the growth axis is located some distance offshore. The initial growth axis forms the reef crest ridge of the present reef and is interpreted as the functional core for reef zonation.



**Ryukyu Islands, Figure 2** Development of modern fringing reef in the Ryukyus. The base diagram is after Kan (2001, 2007) for typical “crest – lagoon” reefs. The accretion style and ages are based on the drilling and trench-wall results in Kume and Minna Islands in the Central Ryukyus. (1): in situ tabular/plately/massive coral framework, (2): rounded coral crusts accumulated in grooves, (3): branching corals and/or platy coral crusts, (4): loose sandy sediments with coral rubble, (5): rubble bed accumulated at the depressed reef substrate.

### Latitudinal gradient in reef geomorphology

The width of reef flats narrows with increasing latitude in the Ryukyu Islands. Changes in reef morphology do not occur gradually but are regionally selective, especially in the width of shallow lagoons that disappear as reef flats become narrower. Hori (1980) used the term “reduction” for the decline in zonation and width of reef flats. The coral species diversity also decreases in higher latitude with loss of the reef geomorphological diversity (Veron, 1992; Nishihira and Veron, 1995).

In the Okierabu Island (27°20'N) in the Central Ryukyu Islands, reef flats are significantly narrower than those in the other islands at similar latitudes where shallow lagoons have not been formed. The reef has been constructed by a uniform facies of in situ tabular corals, which shows that the reef has not experienced any cross-reef energy gradient

(Kan et al., 1995). In the case that the initial growth axis lies at the landward end, the reef experienced no energy gradient during its formation, thus the flat topography with obscure zonation is formed by the following “reef flat accretion” process in the late Holocene.

The width of the reefs are reduced to 100–300 m, partially 500 m in latitudes more than 27°20'N. At the northern limit of the entire reef surroundings of the island is the Kodakara Island located at the latitude 29°13'N. North of this latitude, the reef distributes a part of the coastline. The typical acroporid reef in the Ryukyu Islands gradually disappears around 30°N.

### Summary

The relatively late start-up growth of modern coral reefs in the Ryukyu Islands may be due to the main flow of the



Kuroshio Current inferred to reentering into the East China Sea around 8600 BP ( $^{14}\text{C}$ , Diekmann et al., 2008) along with the high-latitude locality of the archipelago. The development of modern reefs shows the distinct latitudinal gradients in size and distribution until around  $30^{\circ}\text{N}$ . The reef founded in the Iki Island at  $33^{\circ}48'\text{N}$  is a favid reef (Yamano et al., 2001) partially distributing in the area. It is different from the series of acroporid reefs in the Ryukyu Islands and there is a gap of reef development between  $30^{\circ}\text{N}$  and  $33^{\circ}48'\text{N}$ . The gradually disappearing of modern reefs at high latitude along Ryukyu Islands is unique in the global coral reef distribution.

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## Cross-references

[Ecomorphology](#)  
[Emerged Reefs](#)  
[Forereef/Reef Front](#)  
[Fringing Reefs](#)  
[Geomorphic Zonation](#)  
[Holocene High Energy Window](#)  
[Holocene Reefs: Thickness and Characteristics](#)  
[Lagoons](#)  
[Mid Holocene](#)  
[Moats](#)  
[Patch Reefs: Lidar Morphometric Analysis](#)  
[Postglacial Transgression](#)  
[Reef Drilling](#)  
[Reef Flats](#)  
[Reef Structure](#)  
[Spurs and Grooves](#)  
[Submerged Reefs](#)  
[Tropical Cyclone/Hurricane](#)  
[Tsunami](#)

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## SCLERACTINIA, EVOLUTION AND TAXONOMY

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### Definition

Evolution is a widely ranging subject, involving the fossil record, the taxonomic and systematic organization of extant taxa, and the genetic processes that appear to have given rise to those taxa. This article summarizes the main events in the evolution of modern corals, outlines the nature and variation in extant species, and reviews the evolutionary mechanisms most relevant to corals. These are the processes that lead to the taxonomic organization of species and give rise to the taxonomic issues which coral researchers inevitably face.

### Fossil record

The first organisms that might be called scleractinians are known from Paleozoic fossils from China and Scotland (Ezaki, 1998), but the earliest proliferation of organisms that were clearly ancestral Scleractinia are Middle Triassic and consisted of at least seven, but possibly nine, suborders. These corals did not build reefs; they were small solitary or phaceloid organisms of the shallow Tethys of southern Europe and Indo-China (Stanley and Fautin, 2001; Stanley, 2003).

During the Middle and Late Triassic, corals became widespread throughout the Tethys region and their fossils are now found around much of the equatorial Panthalassa Ocean rim. There was an enormous time interval of 20–25 million years between the earliest Triassic corals and the earliest widespread coral reefs. Most noteworthy of Triassic corals is that they had a wide range of skeletal microstructures, suggesting that any common ancestry would

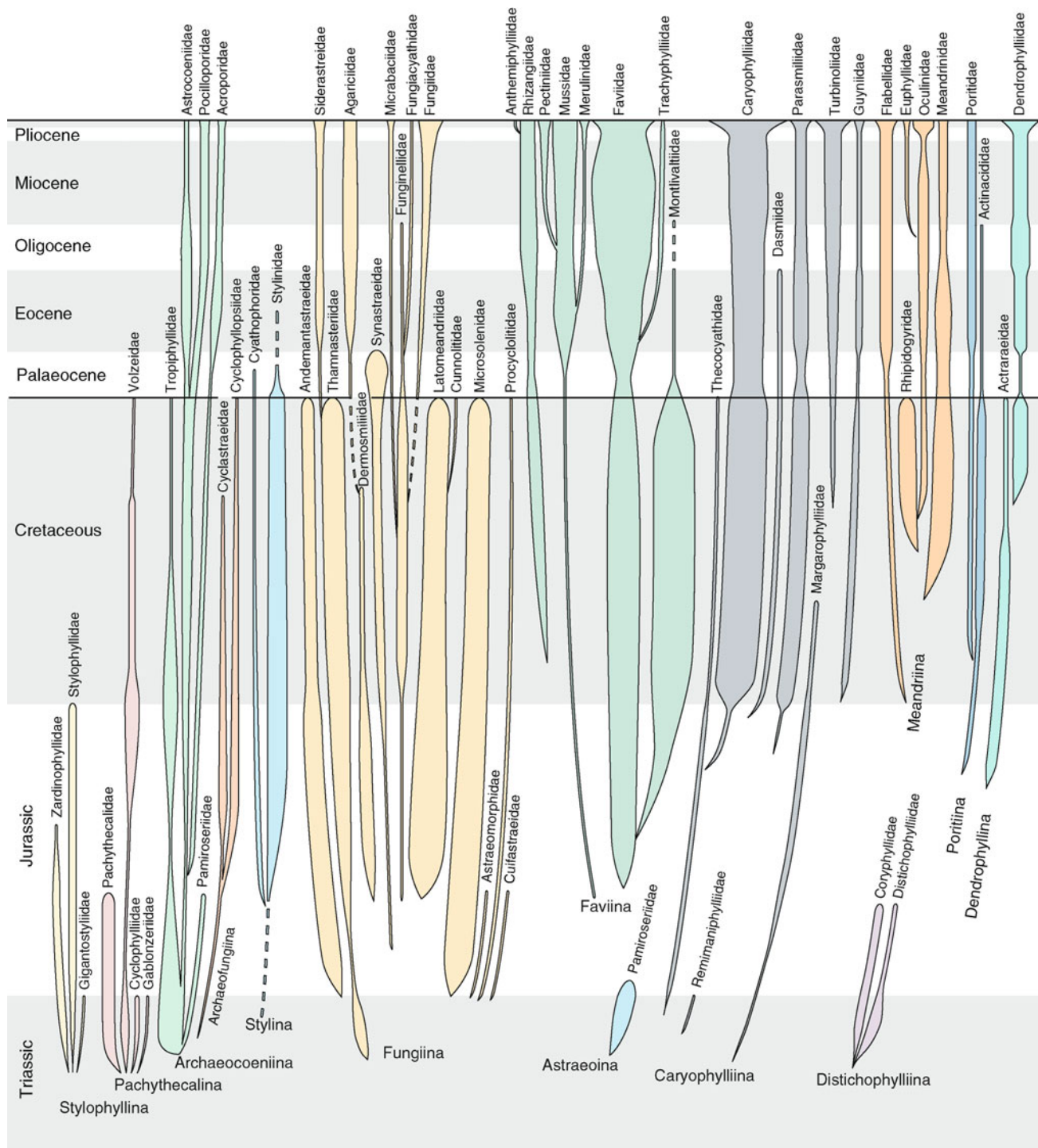
have been remote. Nevertheless, Triassic corals were not the ecological equivalents of modern corals; corallites were large and poorly integrated so that phacelloid growth forms (where branches are composed of individual corallites) were dominant.

There was a 5–8 million year hiatus between the collapse of Triassic reef development and the onset of Jurassic reefs, a time of origin of many new scleractinian families (Beauvais, 1989). The Late Jurassic was probably the all-time global maximum of Mesozoic coral diversity with at least 150 genera recorded in the European Tethys and 51 in the Panthalassa. Paleobiogeographic provinces can be recognized which reflect continental plate movements, especially the increasing width of the Protoatlantic. By the Late Jurassic the paleobiogeographic pattern that had developed was the precursor to the pattern that persisted into the Cenozoic. It was dominated by massive reef development throughout the Tethys, the Atlantic, and also the far eastern Panthalassa. The vast expanse of the eastern Panthalassa was probably a barrier to east-west dispersion, just as the far eastern Pacific is today.

A high proportion of the families of extant Scleractinia have their origins in the Middle to Late Jurassic. For most, the fossil record is not clear, and thus there are few links between the main branches of the Family Tree (Figure 1). The Jurassic was the time of the proliferation if not origin of two of the most major groups of corals, the Fungiina and the Faviina. The Fungiina dominated much of the Jurassic as well as the Cretaceous. As a group it was greatly diminished by the end-Cretaceous mass extinctions and the families attributed to it today have uncertain affinities. The Faviina, on the other hand, are a well-defined group and the Faviidae have remained a major family for 150 million years.

Early Cretaceous corals are broadly similar to those of the Late Jurassic (Beauvais, 1992). However, relatively little is known of the Middle Cretaceous corals. The





**Scleractinia, Evolution and Taxonomy, Figure 1** The 'Family Tree' of Scleractinia. Reconstructing the evolutionary sequences of Scleractinia is a complicated process for it must encompass the fossil records over very great intervals of time, the taxonomic relationships of extant corals, and studies of coral systematics using molecular techniques. The top of the 'tree' (the families of extant corals) is well established, as are the main branches through the Cenozoic, since most of these have extant representatives. However, little is known about the Mesozoic ancestors of Scleractinia, for the majority of families are extinct (simplified from Veron, 2000).

continuity of families indicated in Figure 1 is largely due to extrapolations between Early and end-Cretaceous fauna, with poorly-known families omitted. This is because, by Middle Cretaceous, reefs worldwide had become dominated by rudist bivalves and environmental perturbations greatly affected reef development. It was not until the very late Cretaceous, following an unexplained total extinction of the rudists, that corals returned to a position of dominance. At this time reefs probably again occurred worldwide, but there are few remains of them today.

One-third of all families and over 70% of all genera became completely extinct at the end-Cretaceous boundary. The Faviidae and the Caryophylliidae are the only families that were major component of Mesozoic reefs that also proliferated in the Cenozoic (Veron, 1995).

The evolutionary history of modern corals is divisible into three geological intervals (1) the Paleogene, when the few survivors of the end-Cretaceous extinctions proliferated into a diverse cosmopolitan fauna, (2) the Miocene, when this fauna became subdivided into the broad biogeographic provinces we have today and pre-cursors of most extant species evolved, and (3) the Plio-Pleistocene to present, when the world went into full glacial mode and modern distribution patterns emerged.

For 12 million years after the end-Cretaceous extinctions, only thirteen new genera of corals have been recorded. It was thus a radiation of new zooxanthellate genera that populated the seas of the Eocene. By Late Oligocene, reef development became world-wide and diversity reached an all-time high in the Tethys and Caribbean (Frost, 1981).

The Miocene is the time of origin of non-Oligocene extant genera (primarily Indo-Pacific) and the immediate ancestors of extant species. It is also the time of obliteration of the Tethys, the extinction of non-zooxanthellate corals from the Mediterranean, and the start of the separate evolutionary histories of Atlantic and Indo-Pacific species.

Compared with most other major groups of animals, coral genera are long-lived in geological time and have low extinction rates: nearly half of all extant genera extend

as far back as the Oligocene and nearly  $\frac{1}{4}$  extend back to the Eocene.

The history of corals subsequent to the Miocene (Veron, 1995) becomes decreasingly visible in the fossil record and increasingly visible in the taxonomy and distribution of living corals. The Plio-Pleistocene fossil record of the Caribbean is better than that of the Indo-Pacific and it is in the Caribbean that the impacts of the Pleistocene glaciations were greatest. The progressive closure of the Central American Seaway was one of the most important events in the history of modern corals. Before the closure there may have been no distinction between the corals of the far eastern Pacific and those of the Caribbean. After the closure (3.4 my BP), the corals of the Pacific side of the Isthmus were extinguished, or nearly so.

There are no zooxanthellate scleractinian species common to the Indo-Pacific and the Caribbean today.

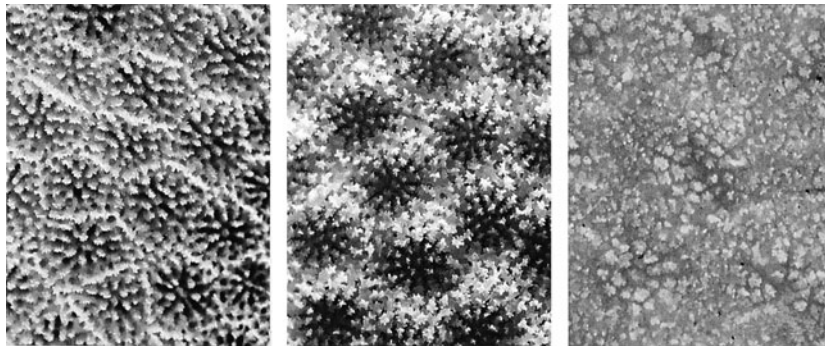
### Species variation

Like most plants, corals have morphological characteristics that vary according to (a) the environment in which they grow, (b) their geographic location, and (c) genetic links among component populations.

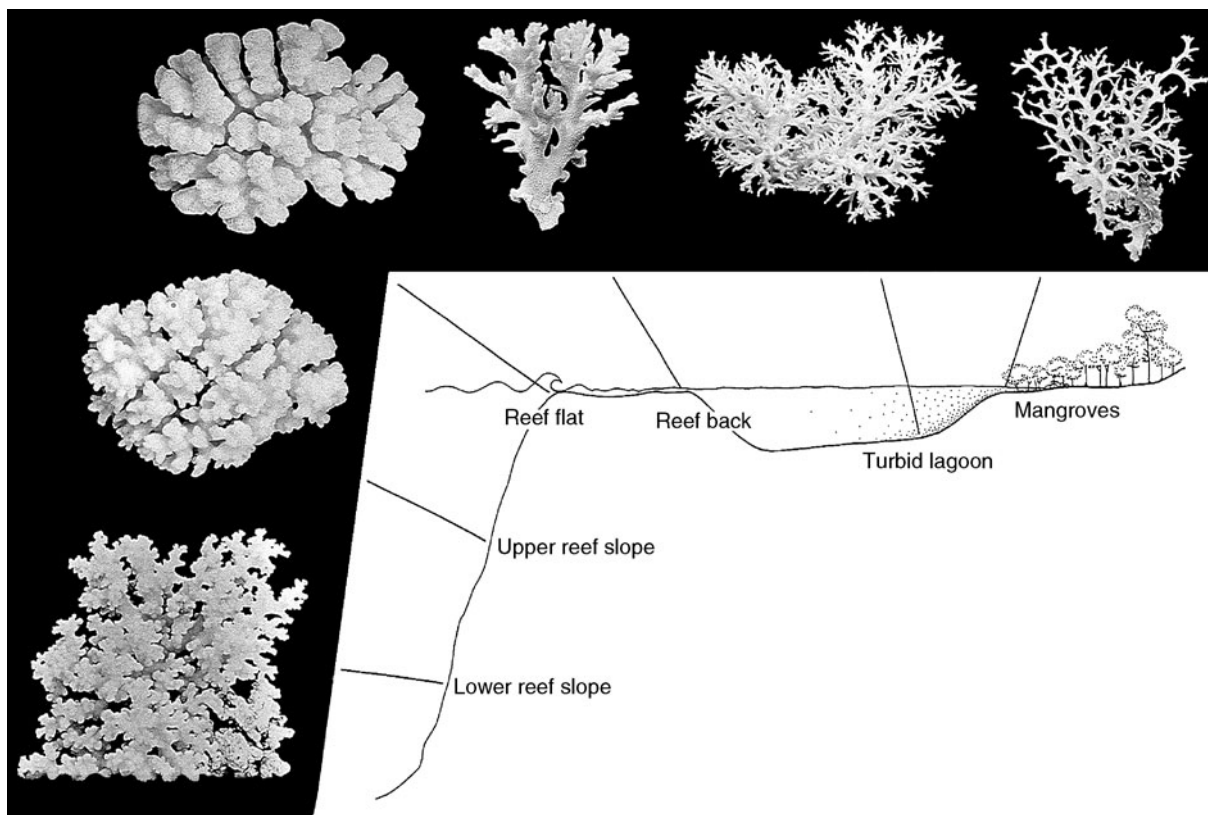
### Environmental variation

Most colonial corals show morphological variation within the one colony. Colonies of some species have variable growth forms which are at least partly genetically regulated independently of environment. However, most species exhibit variations that are clearly associated with different parts of the colony having different micro-environments. Differences among micro-environments include growing space, light availability, sedimentation, and fish grazing. The morphological variations that result affect both growth form and corallite structure (Figure 2).

Different colonies (or individuals) of all coral species vary along environmental gradients (Figure 3). Divers can readily see this happening as they descend down a reef slope. This variation is also seen if a coral is transplanted from one habitat to another. It will usually change its



**Scleractinia, Evolution and Taxonomy, Figure 2** Variation in the structure of corallites in a single specimen of *Porites lutea* ( $\times 10$ ) (After Veron, 1995).



**Scleractinia, Evolution and Taxonomy, Figure 3** Variation in the skeletal structure of colonies of *Pocillopora damicornis* from a wide range of habitats at a single geographic location (After Veron, 1995).

appearance to reflect the conditions of the new habitat. Most plants do likewise; these responses are not under direct genetic control, although particular genotypes may be associated with particular morphologies.

The most important environmental factors controlling growth form are exposure to wave action, levels of illumination, sediment load, and exposure to currents. The different morphologies that result must be accommodated by taxonomic descriptions and understood by persons identifying corals.

### Geographic variation

There are two distinct categories of geographic variation in corals: those which are the outcome of environmental factors, and those which are genetic. Geographic variation that is the outcome of environment is best seen in high latitude coral communities where low temperature and non-reef habitats result in colonies being distinct from their tropical reef-dwelling counterparts. Likewise, there are whole geographic regions where the water is almost always clear (such as the Red Sea or Bahamas) and other regions where the water is usually turbid. Corals from these regions commonly have distinct points of morphological detail that are primarily due to environmental differences.

Geographic variation that is genetically based affects almost all species in some way or other. Again like most plants, the appearance of a single species changes (gradually or abruptly) from one region to the next. These changes may not concern those who are only interested in the species of a single country, but they will definitely concern anybody who tries to identify corals over a wide geographic range. Of more practical importance, it raises significant issues for those who try to identify a species in one country from information about that species from another country.

### Genetic links among populations

It is common for a series of adjacent colonies of the same species, in the same environment, to display a wide range of colors and to have a variety of morphological differences. In such cases, the presence or absence of morphological continuities among colonies, or populations, can be used to distinguish groups of species (commonly called 'sibling species') from a single variable species (commonly called 'polymorphic species'). Although the differences seen are widespread, intermediate colonies can usually be found.

Genetic bridges and barriers generate reticulate patterns in time and space (see below), patterns which maintain the



species' genetic heterogeneity. The taxonomic issues that arise are of endless complexity. They inevitably lead to the conclusion that there are no fundamental differences between species and subspecies taxonomic levels.

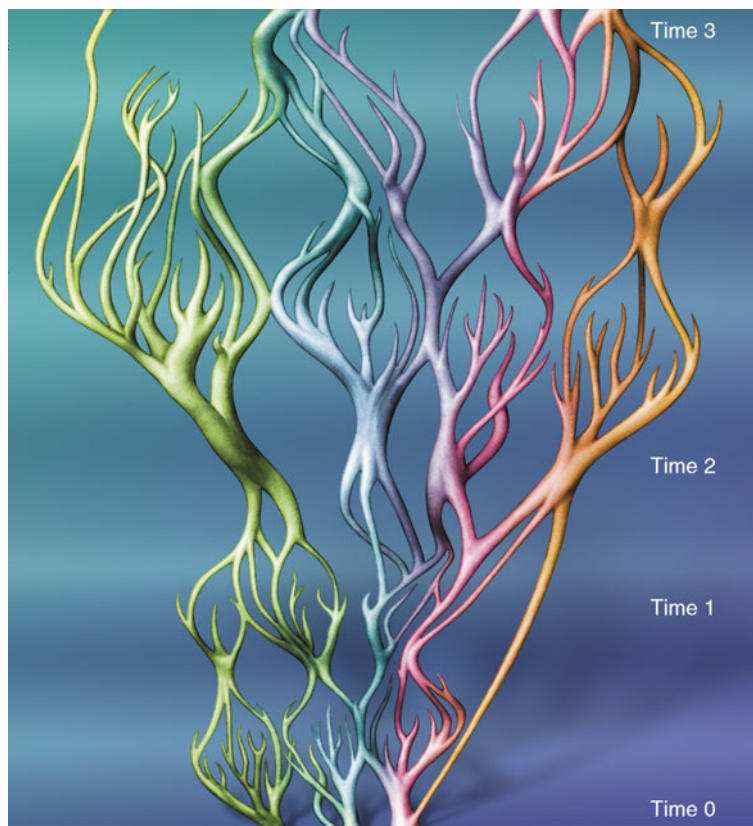
### Evolutionary mechanisms

What happens to geographically variable species in evolutionary time? The issues that arise are not just theoretical. They make it necessary to consider evolutionary change in a way that is very different from that which is generally accepted in both popular and scientific literature. This introduces reticulate evolution, a concept fundamentally distinct from neo-Darwinian evolution, one that involves a different way of looking at what species are and how they change.

### Reticulate evolution

Evolutionary change can seldom be observed directly: it must be re-constructed, as is commonly done using phylogenetic trees (such as [Figure 4](#)). Trees are also one way of envisaging reticulate evolution. Such a tree might have a main trunk for the family, several large branches for genera, and many fine branches for the species. Species that

are currently alive will be the tips of the uppermost branches, and these will be trimmed to uniform height to represent present time. The branch tips, each representing a single species, can be converted into distribution maps, each map representing the present-day distribution of one species. If a single branch (or species) is then sliced into a sequence of horizontal layers, and each layer is turned into a distribution map, each map will indicate the distribution of the species at progressively distant points in time. If the maps are viewed like the pages of a book, the pattern will change sequentially back in time. These changes will not be just distribution changes, they will also be genetic changes occurring in response to changes in ocean currents. As a result, a species (or map) at one point in time is not the same as it is in another point in time: it has been genetically as well as geographically changed. These changes do not occur uniformly, they occur irregularly over the species' geographic range and evolutionary history. Geographic space and evolutionary time interact. The species may break apart, then re-form into a slightly different species. This creates a 'reticulate' pattern in both geographic space and evolutionary time (Veron, 2002).



**Scleractinia, Evolution and Taxonomy, Figure 4** A hypothetical view of reticulate evolutionary change within a group of species. At the bottom (Time 0), the group forms three distinct species each of which is widely dispersed by strong currents. At Time 1, the group forms many indistinct small species units that are geographically isolated because currents are weak. At Time 2, the group forms three species that are again widely dispersed by strong currents. Over the long geological interval to Time 3, the group has been repackaged several times (After Veron, 2000).

As [Figure 4](#) illustrates, basic issues that arise with reticulate evolution are: (a) no species has a time of origin, (b) rates of evolution and extinction are similar over the geological interval represented by the diagram, (c) there are no differences between mainstream species (represented by the thicker branches) and subspecies (represented by thinner branches), (d) there are no differences between 'species' and 'hybrids', (e) the total amount of genetic information represented by the diagram has not greatly changed over time, but has been re-packaged into different 'species' units, (f) extinction occurs through repackaging as well as terminations of lineages.

#### *Ocean currents and reticulate patterns*

Ocean currents are the vehicle of dispersion and the pathways of genetic connectivity. When a species breaks apart (as a result of weak ocean currents) it becomes many species. When it re-forms (as a result of strong ocean currents) it may again be a single species or it may be more than one species. It may also contain genes from other species. This is reticulate 're-packaging', and it occurs constantly at all scales of space and time. Importantly, the re-packaging is not confined to a single phylogeny, it involves many phylogenies simultaneously ([Figure 5](#)).

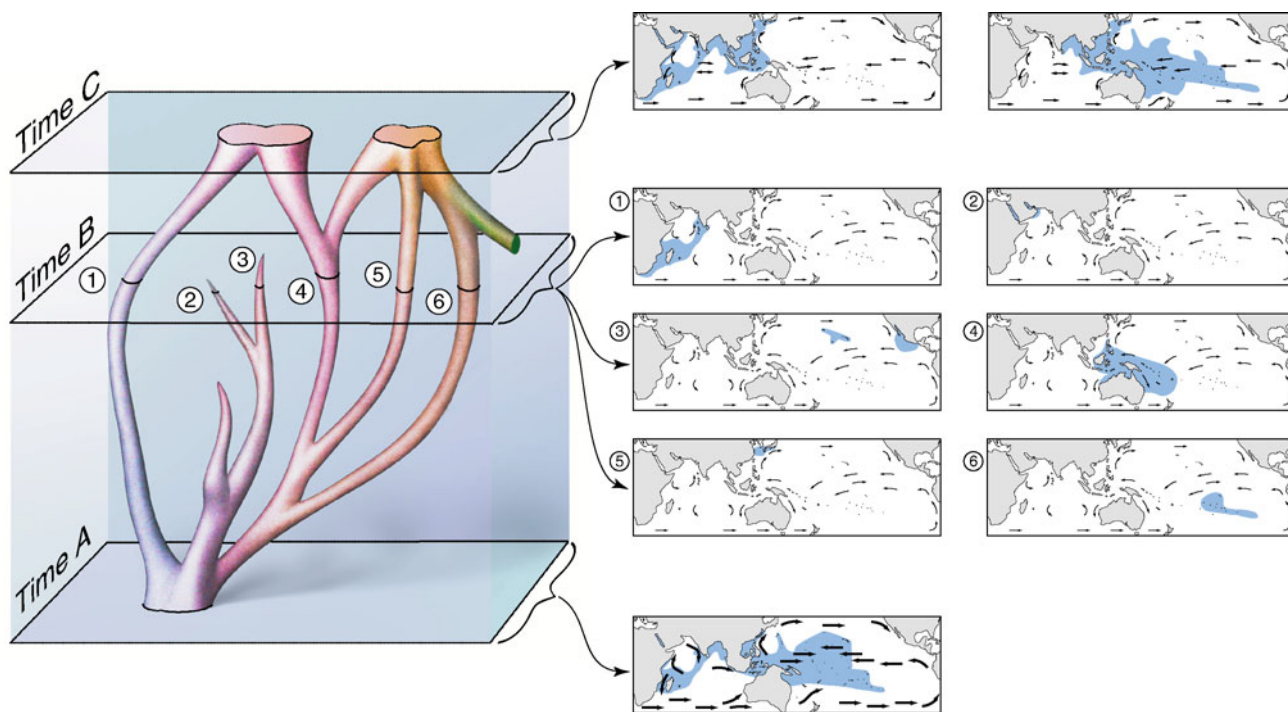
Reticulate evolution is under physical environmental control, not biological control. The physical control changes patterns of genetic connections: it acts on genetic composition. This is again in sharp contrast with a major aspect of the neo-Darwinism where evolution is primarily

controlled by competition between species, a process that creates morphological changes. Reticulate evolution is therefore a mechanism of slow arbitrary change rather than a mechanism for progressive improvement.

Reticulate evolution is primarily driven by changes in surface circulation patterns causing changes to the dispersal patterns of larvae. If currents remained constant throughout evolutionary time, the oceans would be divisible into source areas (where larvae come from) and destination areas (where larvae go to) and geographic gradations within species would be generally predictable. However, with the exception of the great ocean gyres, currents are not constant. Sea levels may fluctuate over 100 m, oceanic passages are opened and closed by tectonic movements, and the Earth goes through cyclical climate changes due to variations in the Earth's orbit around the sun. These, and probably several other types of geoclimatic cycles, cause variations in ocean currents. These changes open and close genetic contacts: they generate reticulate patterns.

The concept of reticulate evolution is highly explanatory of the observations about coral taxonomy and biogeography. It is also strongly supported by all that is known of coral reproduction and is starting to be supported by genetic studies.

The main points illustrated by [Figure 5](#) are as follows. At Time A, currents are strong and the phylogeny exists as a single widespread species. At Time B, currents are weak and the phylogeny has broken up into six



**Scleractinia, Evolution and Taxonomy, Figure 5** A hypothetical view of evolutionary change in a small phylogeny (left) correlated with distribution patterns (maps, right) (see text) (After Veron, 2000).

geographically isolated indistinct or 'sibling' species. (Two of these species (labeled 2 and 3) are doomed to subsequent extinction.) At Time C, currents are strong again and the phylogeny has been re-packaged into two widespread species, which are reproductively isolated. The species on the right is part of the phylogeny of another species. Importantly, there is no distinction between geographic (sympatric) and non-geographic (allopatric) origination, evolution is driven by environmental change, not biological competition (Veron, 2000).

### Competing hypotheses

Theories of biogeography and evolution have always been inter-related. Historically, there have been five main schools:

#### *Darwin's centres of origin*

Darwin (1859) proposed that dispersion was primarily driven by the evolution of new species through natural selection, where older and less competitive species are displaced away from centers of origin to more distant places by fitter and more competitive, descendant species. This is but one aspect of Darwin's theory of the origin of species, yet is one of his most thoughtful for it integrated the known distribution of many plant and animal groups with their fossil record.

Darwin's Centres of Origin theory, or refinements of it, dominated all coral biogeographical thinking until the theory of continental drift appeared to make a fundamental aspect of it – geographic centres – untenable (Briggs, 1984). Interest in this theory, at least as far as corals are concerned, is historical for there are no identifiable centres of origin, only centres of diversity.

#### *Croizat's panbiogeography*

Panbiogeography is very much the subject of Leon Croizat, biogeography's most prolific writer and an outspoken opponent of both Darwin's Centres of Origin and vicariance biogeography (see below) (Croizat, 1981). Panbiogeography is primarily a method (rather than a theory) where 'road maps' of taxa are superimposed to produce 'dispersion highways' (Craw, 1988). The intersection of many highways denotes the existence of 'gates' or 'nodes'. These are places of high connectivity from which dispersion occurs.

Panbiogeography has more relevance to terrestrial life than marine where the base map effectively changes with the vagaries of palaeoclimates, ocean currents and long-distance dispersal (Craw and Weston, 1984).

#### *Vicariance biogeography*

Vicariance biogeography was a major advance on Darwin's Centres of Origin (McCoy and Heck, 1976). It is based on the notion that if one or more barriers form across a species' distribution range, the divided population will diverge in time, forming two or more distinct populations. If these become reproductively isolated they would be two or more distinct species when the barriers

are removed. This process on a large scale would lead to patterns of species that have no centre of origin. Importantly, there is no requirement for dispersion to occur.

Vicariance speciation requires that an ancestral species occupies the geographic area of its descendants and that this area becomes divided up as those descendants progressively evolve. The process, therefore, produces ever-increasing numbers of species, each occupying an ever-decreasing geographic range. The result is ever-increasing endemism, hence a close association between the concepts of endemism and vicariance.

There are significance arguments against vicariance as a general principle in coral biogeography: (a) dispersion is actually of overwhelming importance to corals, (b) the place of origin of coral species is not correlated with place of occurrence, (c) the process of evolutionary change neither commences nor ceases in any particular point in time and (d) there has been no exponential increase in numbers of coral species in any geographic area. On these grounds vicariance cannot be accepted as an evolutionary mechanism in its own right. More importantly, it follows that cladistics as an analytical method must also lead to faulty conclusions as both vicariance and cladistics are based on the same supposition that there is no lateral gene flow (or hybridization) among the species under question (Hennig, 1966; Sober, 1988). Put another way, both vicariance and cladistics are predicated on the absence of syngameon formations (see below).

#### *Dispersion and the founder principle*

The concept of dispersion biogeography, proposed by Mayr (1942) and expanded by Carson (1971), is based on the notion that a species may come to occupy a previously unoccupied place through dispersion (a 'founder' event). It may then be genetically isolated by the formation of a barrier and in time form two or more species. As with vicariance, speciation is allopatric and the outcome is seen in patterns of endemism. The main difference between this theory and vicariance is that this theory requires dispersion to occur and vicariance requires dispersion not to occur. If species co-occur after speciation, additional dispersion is equally necessary for both theories.

Dispersion biogeography is generally linked with Centre of Origin biogeography as the alternative to vicariance (Simberloff et al., 1981) but, as with so much biogeography, this highlights extremes rather than common ground. In reality, most evolutionary issues concerning spatial separation between populations of the same species are irrelevant to corals because of their capacity for long-distance dispersal.

#### *Equilibrium theory*

The equilibrium theory of island biogeography (MacArthur and Wilson, 1963, 1967), an essentially ecological theory, had a major impact on biogeographic concepts when it was first proposed. When rates of immigration to an island are balanced by local extinction, the number of



species (but not necessarily the identity of those species) remains approximately constant. For any particular island there is a dynamic balance between immigration, local extinction, proximity to a continental mainland, and the area of the island. Equilibrium theory has largely gone out of fashion although it is a useful concept for zooxanthellate corals on a regional scale.

### Where reticulate evolution and Darwinian evolution meet

The theory of reticulate evolution, alone among its many rivals, requires no geographic restrictions, does not depend on barriers forming or going and does not result in changes in species diversity. At least as far as corals are concerned, the theory provides a sound reason for observable taxonomic dilemmas (below), is seen in biogeographic patterns, is genetically sound, is reflected in the fossil record and accords well with reproductive biology. As such, reticulate evolution appears to be in direct conflict with Darwin's concept of evolution by natural selection and survival of the fittest, which is at the heart of his almost universally accepted general theory of evolution.

However, these two theories are compatible. It can reasonably be supposed that most life, terrestrial as well as marine, does not exist as reproductively isolated species but rather as syngameons of some sort. (This is seen, for example, in domesticated plants and animals, almost all of which can be artificially hybridized.) These syngameons can undergo change through reticulate evolution, but not natural selection. However, depending on many circumstances, individual species (or genetic units of any kind) may become temporarily genetically isolated, perhaps through the formation of an environmental barrier. If these isolated units become genetically cohesive they would then be able to respond to selective pressure and would be able to undergo Darwinian evolution. The level of isolation required would be unendingly variable among different taxa. If the unit continued to remain isolated it may continue to evolve as a single species or develop into a syngameon. Alternatively, the newly formed unit may in time merge back into the syngameon from which it came. In this case, it will cease to evolve through natural selection. There is, of course, an almost infinite array of such possibilities in the dynamics of life.

### Taxonomy

For over 100 years, species have been considered to be the building blocks of Nature, blocks that have a time and place of origin, which can evolve, and which maintain themselves as discrete entities by being reproductively isolated. This is a logical concept, but one which breaks down, for corals at least, when confronted with the realities of taxonomy and geographic variation. The alternative, where most species have none of these attributes, is initially less intuitive but ultimately is highly explanatory of what can actually be observed in the real world.

### Traditional concepts of species

Concepts of what species are have long been debated, a debate driven as much by misinterpretation as information. This debate has mostly been ignored by taxonomists (who often believe they 'know' what their species are for one reason or another) as well as most other biologists (who often consider it armchair philosophy and thus largely irrelevant to the needs of reality). Be that as it may, species have variously been considered to be (a) self-defining natural units, (b) human-defined units composed of assemblages united by common descent, or (c) genetically-defined units resulting from Darwinian natural selection and/or reproductive isolation. The last involves a group of concepts about species, sometimes called the 'neo-Darwinian synthesis' or the 'biological species concept' (depending on a wealth of detail) that embodies the notions of the building blocks referred above.

### Classification

Forty years ago, museum displays provided much of the scientific basis of what was then known about coral species. The specimens came from voyages of discovery from the tropical world, and they mostly went to the museums of Europe, Japan, and America. At that time, each new form was described as a new species and given a Latin name. Where major collections were made in a single country, the corals were usually given a name that, in practice, had relevance to just that country. As a result, an account of the 'Corals of Japan' was quite different, for example, from an account of the 'Corals of the Marshall Islands', or wherever else.

These accounts were often very different, the main reason being that taxonomists of the time did not have the advantage of scuba diving, thus they had little opportunity to study corals in any natural habitat other than reef flats. They could not, for example, see how a single species gradually changes its growth form down a reef slope in response to decreasing light and turbulence. Most coral taxonomists (and there were many of them) simply concluded that any distinctive growth form was a distinct species.

In all, about 400 taxonomic publications about reef corals, and descriptions of some 2,000 'nominal' species (species in name if nothing else) stem from the pre-scuba era. The issues this raises are many, for the rules of nomenclature state that in most cases the oldest name given to a species is the 'correct' name. Unfortunately, that frequently means that the 'correct' name is based on a poorly described specimen from an unknown environment and sometimes from an unknown country. The author of a new species in those days usually had no concept of what a species might actually be, and they usually had no idea of how their species might vary with environment.

Modern coral taxonomy appears to follow the path of its predecessors, but this appearance is superficial. Taxonomy has become the servant of other disciplines and must

therefore incorporate the many forms of morphological and genetic variations within species that occurs in responses to environment and geographic distance. It should also incorporate, as far as possible, the existence of syngameons.

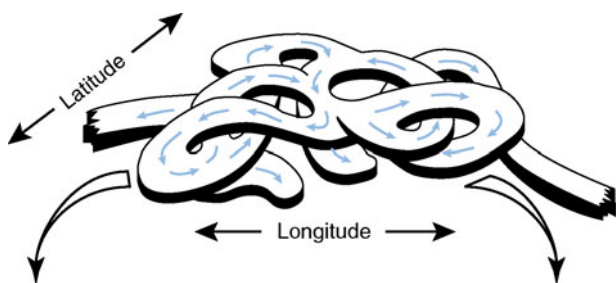
### *Syngameons*

The concept of the syngameon, first recognized by botanists (Grant, 1981) and introduced to the marine world through corals (Veron, 1995), is important for the understanding of the evolutionary mechanisms of corals and the geographic patterns they form. A syngameon, by definition, is a reproductively isolated unit. In concept, so are neo-Darwinian species. In reality, syngameons are nothing like any of the concepts of species referred to above as they incorporate geographic variation and the spectrum of genetic links geographic variation creates among different species (Figure 6).

A syngameon may be a single species, or it may be a cluster of different species which have variable genetic links with other members of the syngameon. Where a syngameon contains several species, a single component species may be distinct at a single geographic location but, because it intergrades with other species at other locations, it will become submerged in a mosaic of variation at other locations. The geographic range and morphological variation of the single 'species' will depend on taxonomic decisions. These decisions will be arbitrary if they impose divisions in natural continua rather than reflect natural units. The syngameon as a whole is not morphologically visible unless its component species are determined genetically or experimentally (through cross-fertilisation trials) in every part of the species' possible distribution range (Veron, 1995).

### *Taxonomic issues*

Geographic variation is far more difficult to study than environmental variation as knowledge of it must be



**Scleractinia, Evolution and Taxonomy, Figure 6** Conceptual paths of gene flow of a single species. Some populations in a species' distribution range are downstream from all other populations. However, most populations import genetic information from upstream locations and export it to downstream locations. This process creates geographic variation within the range of the species and ultimately is responsible for the formation of syngameons (After Veron, 2000).

accumulated from separate studies in different countries: it cannot be directly observed. The main taxonomic issues are: (a) species become progressively less recognizable as single units with increasing geographic range, (b) taxonomists are forced to make arbitrary decisions, (c) synonyms vary geographically. In each case, the more detailed a taxonomic study is, the greater the problem becomes.

### *Taxonomic certainty and geographic range*

With corals as with most plants, most species *do* exist as more-or-less definable units in single geographic regions, such as the Red Sea, the Indonesian/Philippines archipelago, the Great Barrier Reef or the Caribbean. However, widespread species commonly show sufficient geographic variation that they could reasonably be divided into several separate 'sibling species' were it not for the fact that these smaller units form continua. Thus, for example, the majority of species of the Red Sea also occur in Indonesia, but many are sufficiently different in the Red Sea that they would be considered to be distinct species if they were transplanted from the Red Sea to Indonesia (Figure 7).

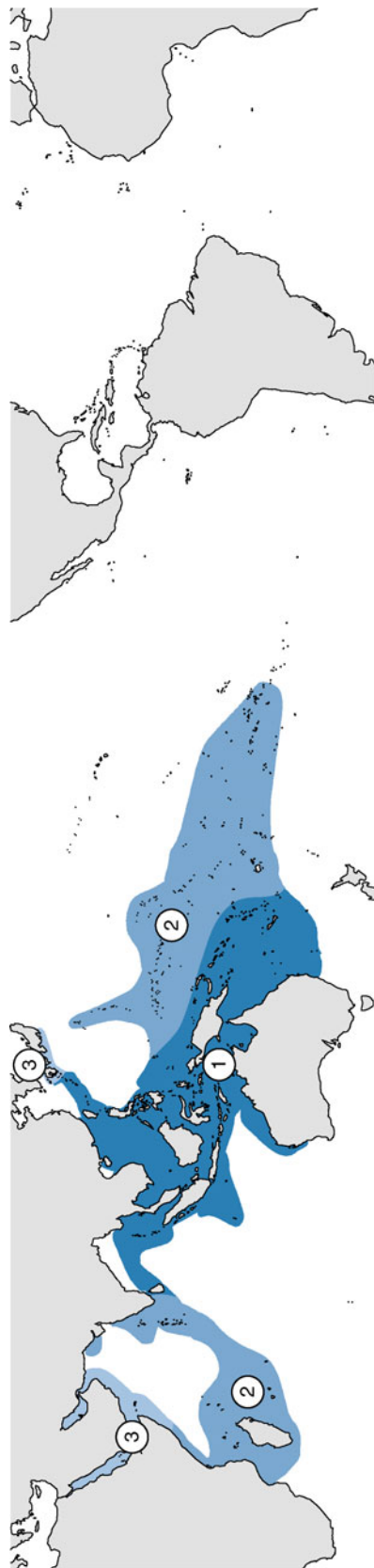
### *Arbitrary decisions*

In theory, taxonomy should accommodate biogeographic patterns. In practice, doing so creates issues like those created when a flat map is projected onto a sphere. The bigger the area of the map, the greater the distortion that results. It is possible to modify the flat map using different types of projections, but this only changes the nature of the distortion.

In traditional taxonomy, geographic variation within a species is accommodated by creating divisions within the species, such as varieties, races or geographic subspecies. In reality, geographic variation repeatedly overrides the morphological boundaries of individual species. In other words, natural continua go beyond the taxonomic or morphological boundaries of single species. This cannot be accommodated by creating divisions within species. The problem remains if the species unit is 'split' into smaller units or 'lumped' into larger units, and it is not solvable by further or more detailed study. Ultimately, the only unit in Nature that is real is the syngameon referred to above.

The reasons why syngameons are not used in taxonomy are (1) they can only be determined with any degree of certainty through exhaustive cross fertilization studies in all geographic regions where their component species occur, (2) they are not likely to have distinguishing morphological characteristics, and (3) they would include so many morphological species that they would need to be re-divided into sub-units of some kind in order to be useful.

This issue will always force taxonomists to make an arbitrary decision as to what a particular species is. Some groups of species may be distinctive in some geographic regions and not in others. The outcome of detailed studies of these species may either be a single 'species complex' or a group of similar species. In either case, species descriptions and distribution maps artificially simplify the reality of the complex.



**Scleractinia, Evolution and Taxonomy, Figure 7** Geographic variation from a taxonomic point of view. A species that is taxonomically straightforward in the central part of its range (area 1) may have morphological uncertainties in more peripheral parts (area 2) and form distinct subspecies at extremities (area 3) (After Veron, 2000).



### Geographic variation in synonymies

Synonymies are intended to clarify the taxonomic history of an individual species and as such are commonly considered to be a formal statement about the status of that species. However, if species can vary geographically it follows that detailed synonymies may also vary geographically. In practice, this consideration is seldom taken into account.

### Summary

The above considerations argue that the term 'species' can legitimately have a wide range of meanings. Within a single region, species are usually morphologically distinguishable from other species and are genetically semi-isolated from other species. Over their full geographic range, species vary morphologically and genetically and are not necessarily morphologically or genetically isolated from other species. Geographic patterns of species combine with distribution changes to produce networks of genetic links. These links are not observable in single geographic regions and for this reason are not generally recognized in taxonomic studies of corals or most other groups of organisms.

In theory at least, corals vary according to the spectrum of habitats they occupy, the size of their geographic range, and the extent of gene flow within that range. In practice, variation that is correlated with habitat (such as the variations of *Pocillopora damicornis*, [Figure 3](#)) can be satisfactorily described and illustrated so that the species is a single identifiable unit. However, genetic variation defies the use of units if they merge with other units. When this happens, the units can only have arbitrary boundaries. This certainly happens with corals and probably does so with most other marine life.

General principles about species over large geographic ranges are: (1) their geographic boundaries merge with other species, (2) their morphological boundaries merge with other species, (3) there are no definable distinctions between species and subspecies taxonomic levels ([Veron, 1995](#)).

Nature, therefore, is mostly composed of continua in space and time, continua which will always defy human attempts to make taxonomic units. If taxonomists create units (as they must if their taxonomy is to be meaningful) it must be remembered that these units are artificial: they lack discrete morphological boundaries, and they also lack discrete geographic boundaries. Also, as our knowledge of coral biology increases, it is becoming clear that the ecological, physiological, and reproductive characters of individual species also vary geographically. It is a human dilemma that we need taxonomic units at all to communicate information about Nature's organization, when Nature is not necessarily divided into units of any kind.

### Acknowledgments

The author thanks Dr. M.G. Stafford-Smith for critically reviewing the manuscript.

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### Cross-references

[Corals: Biology, Skeletal Deposition, and Reef-Building](#)  
[Corals: Environmental Controls on Growth](#)  
[East Indies Triangle of Biodiversity](#)  
[Diagenesis](#)  
[General Evolution of Carbonate Reefs](#)  
[Mass Extinctions, Anoxic Events and Ocean Acidification](#)  
[Taphonomy](#)  
[Tethys Ocean](#)

## SCLEROCHRONOLOGY

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### Synonyms

Coral chronometers; Related to Dendrochronology

### Definition

**Sclerochronology:** The term sclerochronology is derived from the Greek words *sklero*, meaning “hard,” and *chronos*, meaning “time.” The field of sclerochronology is the study of periodicities stored in accreted hard parts and skeletons of various extant and extinct organisms. The periodicity can range from daily to annual scales and compose chronologies that span years to centuries, thus providing potentially long records of historical variations. Annual periodicity provides a chronology for determining age, growth rates, and reconstructions of environmental influences. Along with the recorded growth chronologies, the chemical composition of the skeleton also contains temporal records based on isotopic ratios and trace elemental concentrations, which can be used to reconstruct proxy paleoenvironmental and paleoclimatic records. Studies of skeletal growth and geochemical records have been used within the broader fields of ecology, physiology, and paleoclimatology. Sclerochronology is akin to the study of annual growth rings in trees, termed dendrochronology.

### Introduction

Sclerochronology encompasses a wide array of organisms within coral reef environments that secrete structures which reflect growth periodicities. These may include, but are not limited to: corals, mollusks, fish, and sclerosponges. The following description is constrained to coral sclerochronology to provide a more focused perspective within the broader field of sclerochronology. It should be noted that early developments in mollusk sclerochronology (Isely, 1913, 1931; Orton, 1923; Davenport, 1938; Bonham, 1965) and fish sclerochronology (Leeuwenhoek, 1685; Pell, 1859; Adams, 1940; Jackson, 2007) paralleled the advances in coral sclerochronology, but because the nature and skeletal correlates of annual records differ substantially between taxa and phyla, descriptions and methods are generally specific to each subfield of sclerochronology.

Scleractinian corals are colonial organisms that secrete calcareous skeletons composed primarily of calcium carbonate, i.e., aragonite. In many species, the coral skeletons possess internal growth banding, density banding, and/or external growth ridges, which record the growth rate of the colony. Coral colonies can live hundreds of years and therefore provide annual chronologies of growth rates over time in response to changing environmental

conditions. Coral sclerochronology encompasses the study of annual density band formation, historical growth records, and reconstruction of environmental records based on density band chronologies and skeletal chemistry of stable isotopes and trace elements.

### History

The term sclerochronology first appeared in the published literature in 1974 when Buddemeier et al. proposed: “Similar potentials have already been realized in the case of dendrochronology (Fritts et al., 1971); an analogous approach to the study of growth patterns in calcareous exoskeletons or shells could be designated sclerochronology” (Buddemeier et al., 1974). This was followed by a paper in 1976 entitled “Sclerochronology: a tool for interpreting past environments” (Hudson et al., 1976). Though the term sclerochronology may have arisen in the 1970s, the field of study has origins dating back to the nineteenth century when initial observations consisted of the apparently cyclical ridges on the external coral surface that were associated with periodic growth of the colony.

In 1898, referring to *Madrepora palmata* (*Acropora palmata*, Lamarck 1816), R. B. Whitfield remarked “Another feature worthy of mention is seen over all the larger spreading fronds in the form of broad undulations. These mark periods of growth, being thicker and thinner in substance, and are undoubtedly annual growths of the coral, . . .” (Whitfield, 1898); see Figure 1. In an effort to relate these “annual” growth patterns on the colony surface to environmental controls, Whitfield further speculated that they were a result of seasonal variations in water temperature. Vaughan (1915) later confirmed that these surface undulations were in agreement with annual growth rates for this species in the same locale.

Many of the early studies measured coral growth rates, though not directly from skeletal records, in order to address fundamental relationships between coral growth, environmental influences, and reef accretion (Finckh, 1904; Wood Jones, 1908; Mayor, 1918; Edmondson, 1929; Stephenson and Stephenson, 1933; Tamura and Hada, 1934). Much of this work, coupled with observations of cyclical skeletal ridges, led to the concept that corals may present useful chronometers of historical environmental, climatic, and even astronomical change (Wells, 1963; Runcorn, 1966; Shinn, 1966). The utility of corals as chronometers, suggested by these authors, was based on external growth ridges and directly measured growth rates; however, it was not based on internal variations of the skeletal architecture that produce annual density bands, which has come to be the most widely utilized characteristic in coral sclerochronology.

In 1933, the Chinese paleontologist, Ting-Ying H. Ma was the first to note that the internal skeletal architecture of Paleozoic corals (Silurian, Middle and Upper Devonian, and Lower Carboniferous) exhibited periodic variations in the size and densities of skeletal elements (dissepiments and tabulae), which appeared to reflect an annual cyclicity,



**Sclerochronology, Figure 1** Example of external growth ridges on *Acropora palmata* reported by R. B. Whitfield in 1898.

and further asserted that these variations were in response to seasonal climatic changes, in particular water temperature (Ma, 1933). Using modern corals, *Favia speciosa* from Japan, Ma found similar patterns characterized by variations in dissepiment thickness and spacing, which appeared as repeating bands within the skeleton (Ma, 1934a, b). Using these internal growth bands, Ma measured growth rates and deduced temporal relationships between growth rates and temperature, where higher growth rates were associated with warmer years and lower growth rates with cooler years. Ma (1937) also assessed corals from different regions (Pacific, Atlantic, and Indian Oceans) and found a spatial relationship between growth and temperature, where corals growing in regions of warmer temperature grew faster than that in regions of cooler temperature. Ma's research represents the first assessment of internal growth banding, a precursor to studies of annual density banding, as well as the spatial and temporal relationship between coral growth rates and water temperature.

A significant advancement in coral sclerochronology occurred in 1972 when Knutson et al. confirmed the annual nature of density banding using corals from Eniwetok Atoll, which were exposed to nuclear weapons testing fallout (Knutson et al., 1972). A combination of X-radiography and radioautography (Bonham, 1965), termed autoradiography by Knutson et al., was used to identify density banding and radioactivity banding, respectively, within medially sectioned skeletal slabs from the coral colonies. The number of density bands in between, and following, the radioactivity bands corresponded with the number of years between nuclear weapons detonations and the date of coral collections, thus providing a straightforward proof of the annual nature of coral density banding. Shortly thereafter, the annual nature of density banding was reconfirmed for different species and by radiometric analysis (Dodge and Thomson, 1974; Moore and Krishnaswami, 1974) and radiometric, staining, and direct measurement (Macintyre and Smith, 1974). Once the basic premise that coral skeletons possessed annual density bands had been established, the field of sclerochronology expanded quickly with novel approaches aimed at developing and understanding the measurement of linear extension rates, bulk

density, and calcification rates, the skeletal structural basis of density banding, environmental correlates of growth rates, coral growth ecology, and the impacts of climate change on coral growth rates.

Prior to the discovery of annual density banding, the chemical composition of coral skeletons had been analyzed for Ca and Sr (Thompson and Chow, 1955), Sr, Ca, and Ba (Bowen, 1956), Co, Ag, and U (Veeh and Turekian, 1968), C and O isotopes (Keith and Weber, 1965; Weber and Woodhead, 1970), Sr, U, Ba, Cu, B, Li, and Zn (Livingston and Thompson, 1971); however, geochemical analyses of coral skeletons as a chronological record had yet to be developed. Similarly, Ra, Th, and Pb were used as a radiometric confirmation of annual density banding, but it was not until the late 1970s when annual chronologies from density banding and geochemistry were used together to derive proxy environmental records (Goreau, 1977; Emiliani et al., 1978). Fairbanks and Dodge (1979) demonstrated annual periodicities in C and O isotopes, which illustrated the sclerochronological reliability and potential for proxy records of temperature stored within the chemical composition of the skeleton. Since this time, research into isotope fractionation, incorporation of trace elements, and the application to proxy reconstructions have rapidly expanded providing extensive contributions to the fields of paleoclimatology, ocean circulation, and climate change (Swart, 1983; Druffel, 1997; Gagan et al., 2000; Swart and Grottoli, 2003; Grottoli and Eakin, 2007).

Fluorescence of the coral skeleton was initially suggested as a recorder of coastal rainfall by P. J. Isdale (1984) (Boto and Isdale, 1985). Though the nature of these fluorescent bands has been brought into question as a possible artifact of skeletal density variations (Barnes et al., 2003; Barnes and Taylor, 2005), skeletal fluorescence (luminescence) has been reported to provide records of runoff (Isdale et al., 1998; Lough et al., 2002), precipitation (Fang and Chou, 1992), and wind speed (Nyberg, 2002), monsoon climate and upwelling (Tudhope et al., 1996), mortality (Hendy et al., 2003), El Niño Southern Oscillation teleconnections (Hendy et al., 2003), rainfall and river flow (Lough, 2007), and hurricane activity (Nyberg et al., 2007).

### Growth measurements from density banding

Coral samples for sclerochronology were originally collected as whole colonies; however, the currently preferred method is to collect cores (5–10 cm in diameter) using pneumatic or hydraulic drills (Figure 2) due to the minimal impact on coral colonies when cores are replaced with appropriate plugs. The cores are sectioned into 0.4–0.8-cm thick parallel-sided slabs oriented along the primary growth axis. The slabs are then planed to precise thickness for accurate density determination. Slabs are rinsed profusely after cutting and planing to remove all loose debris that can affect densitometry and geochemical sampling. Methods and quality of X-radiography will vary greatly based on the type of X-ray machine used; however, as a general rule, longer exposure times using slow speed



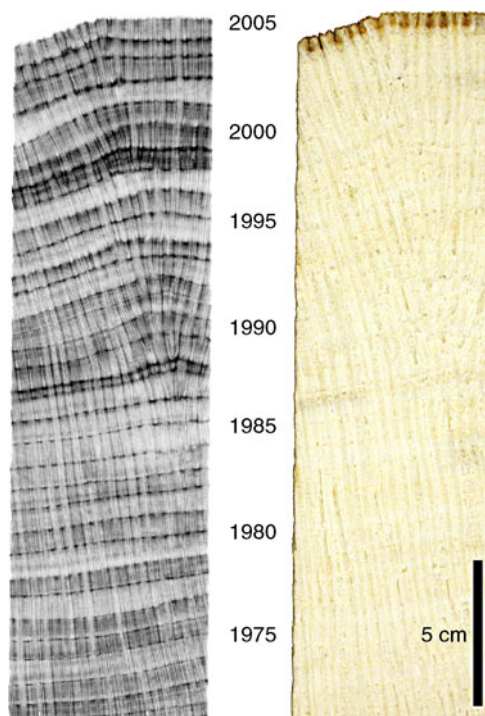


**Sclerochronology, Figure 2** Coring of a coral colony using a hydraulic drill to obtain a skeletal record of coral growth rates.

film with a small grain size will produce the highest quality X-radiographs. As an example, using an industrial X-ray film at a source to object distance of  $>1$  m and X-ray machine settings of 70 kVp, 15 mA, and exposure times of 5–10 s will provide good X-radiographs (Figure 3).

Density banding is revealed on X-radiographs of skeletal slabs and is apparent as alternating light (high-density) and dark (low-density) bands on the X-radiograph. A couplet of light and dark bands represents a single year's growth and is most often referred to in the singular form as an annual band. The annual nature of density banding allows three parameters of coral growth to be determined: (1) linear extension rate, (2) bulk skeletal density, and (3) calcification rate. Assessing all three growth parameters provides the most complete understanding of coral growth, and no one parameter is universally representative of the others (Dodge and Brass, 1984).

The annual extension rate is measured from the top of one high-density band to the top of the next high-density band and presented in units of cm/yr. The first extension rate measurements were collected on X-radiographic positive prints using dial calipers and following a linear transect normal to the density bands and along the axis of maximal growth; see review of early growth studies in Buddemeier and Kinzie (1976). X-radiograph densitometry (Buddemeier, 1974; Dodge and Thomson, 1974; Chalker et al., 1985) and gamma densitometry (Chalker and Barnes, 1990) provide  $xy$ -data of density and distance along the coral slab, which can also be used to determine



**Sclerochronology, Figure 3** X-radiographic positive print with annual density banding (dark bands = high-density, and light bands = low density) and a photograph of the coral slab.

extension rates based on distance from one density maxima (or minima) to the next density maxima (or minima). Annual values can also be derived from the combination of adjacent high-density and low-density bands. Density data can be delimited into high-density and low-density bands by the midpoint, or average value, between maxima and minima and by the zero crossing of the second derivative of the density data, which is the inflection point between bands. High-density and low-density data provide information about growth rates, which may vary independently on a seasonal basis.

Density measurements of coral skeletons are best described as the bulk density over the thickness of a coral slab, as opposed to the density of calcium carbonate skeleton. Density data is presented in units of  $\text{g/cm}^3$ . The density of coral skeletons has been measured by a variety of techniques, including X-radiograph densitometry (Buddemeier, 1974; Dodge and Thomson, 1974; Chalker et al., 1985), gamma densitometry (Barnes and Devereux, 1988; Chalker and Barnes, 1990), computerized tomography (Bosscher, 1993; Bessat and Buigues, 2001), buoyant weight technique (Dodge et al., 1984; Barnes and Devereux, 1988), weight and volume (Highsmith, 1979), and mercury displacement (Dustan, 1975).

X-radiograph densitometry, a common method of density determination, is based on the principle that when two materials (e.g., a coral sample and an aluminum standard) are X-rayed and the exposed film exhibits equal optical density for both materials, the density of the sample material can be calculated. Buddemeier (1974) obtained the mass absorption coefficients for both the sample and standard from tabulated values; however, this technique required the exact determination of the applied X-ray voltage and was further complicated by the assumption of an effective X-ray beam energy and the inhomogeneity of the sample and standard. Chalker et al. (1985) avoided such problems by using relative mass absorption coefficients. They determined the relative mass absorption coefficient of the standard and sample by slopes of curves fitted to data of sample thickness vs. densitometer output voltage. Dodge and Kohler (1985) adapted these methods to image processing, which replaces the densitometer output voltages with gray-scale pixel values (0–255), which are converted to relative optical density (ROD) values. The values are not measurements of true optic density (OD), which ranges from 0.0 to 4.0, because OD requires measurement of the incident light intensity before passing through the X-radiograph (Carlton and Adler, 1996).

Once extension rates and density have been measured, the calcification rate is calculated as the product of extension and density and is presented in units of  $\text{g/cm}^2/\text{yr}$ . The calcification rate is a measure of the addition of mass, for a give area, over time, with the three growth parameters related by the formula:

$$\text{Extension (cm/yr)} \times \text{density (g/cm}^3\text{)} = \\ \text{calcification (g/cm}^2\text{/yr)}.$$

## Skeletal basis of density banding

The construction and growth of coral skeleton is based on the formation of aragonite crystals, at sites of calcification, which are organized into fan-shaped structures called sclerodermites, and represent the building blocks of skeletal architecture (Wells, 1956). The formation of aragonite crystals exhibits a diel pattern, where well-organized and closely arranged needles are formed at night and loosely arranged needles are formed during the day (Barnes, 1970; Gladfelter, 1983). These diel patterns in skeletal accretion produce daily external growth ridges (Barnes, 1972), which have been used as evidence for variation in the number of days per year from the Middle Devonian to present (Wells, 1963). Though daily growth ridges represent a valuable trait for sclerochronology, they are substantively different than the skeletal variations responsible for X-ray revealed annual density banding.

Buddemeier (1974), in his X-radiographic studies of coral skeletons, determined that variations in organic content nor trace element levels were substantial enough to cause the density variations associated with banding and proposed two alternatives for density-band formation: (1) the orderliness in which aragonite needles are deposited, and (2) the variation in size and spacing of the skeletal elements. Barnes and Devereux (1988) presented terminology for categorizing the scale of skeletal variations referring to the organization of aragonite crystals or needles as “microarchitecture” and the organization of skeletal elements (e.g., dissepiments, septa, and thecae) as “meso-architecture.” Barnes and Devereux analyzed the density of coral skeleton (*Porites* sp.) by gamma-densitometry, buoyant weight, and powdered skeleton techniques and found that variations in microarchitecture were insufficient to account for density banding and further suggested that variations in the skeletal mesoarchitecture were responsible for density banding.

Skeletal structures reported to vary in conjunction with density bands include thickness and orientation of trabeculae (Buddemeier and Kinzie, 1975), dissepiment thickness (Macintyre and Smith, 1974; Emiliani et al., 1978), dissepiment and costae thickness (Dodge et al., 1992), and septa and columellae thickness (Helmle et al., 2002), and a general thickening of all skeletal elements (Barnes and Devereux, 1988). It is generally accepted that periodic thickening and/or coalescing of skeletal structures are responsible for density banding and also that the specific structures responsible for producing density bands vary between genera and species. The impact skeletal structures have on the attenuation an X-ray beam passing through a coral slab and the resulting density bands (or false bands) on the X-radiograph has been described by experimental, theoretical, and modeled approaches (Barnes et al., 1989; Barnes and Lough, 1990; Barnes and Taylor, 1993; Taylor et al., 1993; Le Tissier et al., 1994).

## Causes of density banding and correlates of coral growth

The environmental or endogenous causes of annual density banding have not been clearly identified. Common hypotheses include temperature, light, productivity, and reproduction. Annual reproductive cycles may cause a metabolic shift from growth to gamete productions, larval development, or tissue repair from spawning. Mendes and Woodley (2002) found *Montastraea annularis* corals from Jamaica, which underwent a bleaching event in 1995–1996, failed to produce a high-density band in 1996 and suggested this was due to the lack of gonad development and spawning in 1996. Alternative explanations for this event could include the bleaching stress, lack of photosynthetic energy contributions, or exceptionally high temperatures. Mendes (2004) conducted a controlled experiment considering temperature, light, and reproduction relative to density banding and concluded that reallocation of energy from growth (extension rate) to reproduction (gonad size) was the likely cause of high-density band formation in *M. annularis* from Jamaica, which occurs in late August to early October. It is important to consider that gonad size, temperature, and light were all at their highest levels during the period of high-density band onset. Characteristics of temperature, light, and spawning cycles generally correlate (Mendes, 2004; van Woesik et al., 2006), which makes it difficult to disentangle the true cause of density band formation.

Temperature and light are the two most commonly cited limiting controls on coral growth rates and therefore are likely to play a dominant role in controlling subannual growth rates responsible for density banding. Weber et al. (1975) and Highsmith (1979) attributed density banding primarily to temperature with high-density bands forming when temperatures were at their peak. Buddemeier (1974) demonstrated strong correlation between density banding and precipitation though he attributed this primarily to the influences of light availability. Klein and Loya (1991) cited temperature and light as combined factors controlling density band formation. Wellington and Glynn (1983) found that light was a better correlate with high-density band formation and further suggested that density banding may be controlled by combined effects of light, productivity, and reproduction. Varying with temperature and light, autotrophic (photosynthesis) and heterotrophic (feeding) energy contributions may control metabolic resources in a cyclical pattern, thus giving rise to annual density banding. Klein et al. (1993) reported that timing of density band formation varied by depth (3 m, 30 m, and 51 m) and attributed this observation to autotrophy/heterotrophy ratios. Temperature and light might also control density banding through the energetic contributions of photosynthesis, where  $P/R$  ratios may exceed a threshold for photosynthetic contributions during the summer temperature maximums and/or when light levels exceed a similar threshold.

Correlations between environmental parameters and coral growth records derived from density banding have

included extension rates alone, as well as complete growth assessment, including density and calcification. Correlations of coral growth with environmental variables include depth and light vs. extension (Hubbard and Scaturro, 1985; Huston, 1985; Logan and Tomascik, 1991; Bosscher and Meesters, 1993; Logan et al., 1994); light vs. extension, density, and calcification (Wellington and Glynn, 1983); temperature vs. extension (Jokiel and Coles, 1977; Dodge and Lang, 1983; Guzman and Tudhope, 1998); temperature vs. extension, density, and calcification (Highsmith, 1979; Lough and Barnes, 1997, 2000; Carricart-Ganivet, 2004; Worum et al., 2007; Cooper et al., 2008; Lough, 2008; De'ath et al., 2009); hydraulic energy vs. extension, density, and calcification (Scoffin et al., 1992); precipitation vs. extension (Buddemeier et al., 1974; Fang and Chou, 1992); nutrients vs. extension (Tomascik and Sander, 1985; Klein et al., 1993), and nutrients vs. extension, density, and calcification (Wellington and Glynn, 1983). Coral skeletal records have also been used to assess growth responses to anthropogenic perturbations such as crude oil and oil dispersants (Lewis, 1971; Knap et al., 1983) and runoff and coastal development impacts from turbidity, sedimentation, and sediment resuspension (Dodge et al., 1974; Loya, 1976; Dodge and Vaisnys, 1977; Barnes and Lough, 1999; Carricart-Ganivet and Merino, 2001; Torres, 2001).

Coral sclerochronology is not rooted in a mechanistic understanding of the growth-limiting controls over varying temporal and spatial scales and is therefore prone to errors associated with causation inferred from correlation. No single environmental parameter has been demonstrated to consistently and fully explain the annual variability in extension, density, or calcification, and it is likely that the limiting controls on coral growth are a combination of environmental influences that interact on daily to decadal periods over varying spatial scales. Effective sclerochronology aims to better identify these interactions for constrained time periods and a defined ranges of influence.

## Coral growth and climate change

Skeletal deposition of corals and ultimately coral growth rates are generally controlled by environmental and climatic conditions and the chemical composition of the surrounding water. With regard to recently rapid climate change, influences from rising sea surface temperatures and increasing atmospheric carbon dioxide levels have potentially affected coral growth over recent years. Increased carbon dioxide levels have lowered the pH of oceanic surface waters with resultant decreases in the aragonite saturation state (Gledhill et al., 2008), which has been hypothesized to cause decreases in calcification rates of corals and other calcifying organisms (Smith and Buddemeier, 1992; Kleypas et al., 1999). Increased sea surface temperatures are known to exert a positive influence upon coral growth rates (Weber et al., 1975), which



occurs both on spatial (Lough and Barnes, 2000) and temporal (Lough and Barnes, 1997) scales. However, coral growth is also negatively influenced by the metabolic effects of coral bleaching, which occurs above their thermal tolerance (Jokiel and Coles, 1977; Goreau and Macfarlane, 1990).

Records of coral growth consisting of extension, density, and calcification are predominantly short-term, decadal-scale, analyses used to assess site-specific growth ecology (Wellington and Glynn, 1983; Dodge and Brass, 1984; Lough and Barnes, 1992; Scoffin et al., 1992; Carricart-Ganivet et al., 2000; Carricart-Ganivet and Merino, 2001; Worum et al., 2007). Long-term coral growth records have generally been limited to extension rate measurements alone (Hudson et al., 1976, 1994; Dodge, 1981; Hudson, 1981; Dodge and Lang, 1983). Relatively few studies have measured all three parameters of growth for long-term, multidecadal to century-scale records. Lough and Barnes (1997) and Bessat and Buigues (2001) measured extension, density, and calcification over century-scale records and reported a positive relationship between sea surface temperature and calcification over the twentieth century. However, Lough (2008) reported recent declines in 5-year averaged calcification and extension between 1965 and 2005 despite increasing sea surface temperature over the same period. De'ath et al. (2009) analyzed ten multicentury growth records in combination with many shorter and more recent coral growth records (up to 328 colonies) and identified a 14% decline in calcification and 13% decline in extension since 1990. Recent declines in calcification have also been reported in two short-term studies (Cooper et al., 2008; Tanzil et al., 2009). The recent declines reported from coral records of extension and calcification suggest that the positive relationship between sea surface temperature and calcification over the twentieth century may not be holding up under current environmental conditions and that further analyses are necessary to assess the range of these reported declines in coral growth and the role aragonite saturation states may play in these declines.

## Summary

The field of coral sclerochronology arose from initial observations of external growth ridges, variations of internal skeletal structures, and apparent relationships between environmental conditions and coral growth. The confirmation of the annual nature of density banding led to modern methods of X-radiography, densitometry, and measurement of growth parameters: extension, density, and calcification. Coral sclerochronology has demonstrated its utility by advancing our understanding of coral growth ecology along with anthropogenic impacts and environmental influences on growth rates. The skeletal basis of density banding revealed on X-radiographs is well described; however, the fundamental cause of density banding has yet to be clearly defined. Based on decades of published research on coral growth rates and

environmental influences, it is clear that coral growth is not a fully controlled by a single environmental limiting factor, in contrast to the analogous field of dendrochronology. The value of coral sclerochronology lies in the ability of corals to store records of growth in their skeleton, over long periods of time, which reflect the sum total of environmental and climatic controls. The field of coral sclerochronology is continually advancing and provides unique records, throughout the tropical and sub-tropical oceans, of potential climatic/environmental change and anthropogenic influence.

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## Cross-references

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## SEA LEVEL CHANGE AND ITS EFFECT ON REEF GROWTH

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## Introduction

Over short timescales (minutes to months), sea level changes with tides, waves, atmospheric pressure, wind, and currents. Mean sea level (hereafter “sea level”) is the average level of the sea surface over a specific period (e.g., 1 year) after filtering out these short-term fluctuations. Sea level is determined from a reference level on land (e.g., a benchmark), and defined as an equipotential surface of the gravity field (i.e., the geoid).

At longer timescales (longer than a decade), sea level varies with changes in the volume of seawater and shape of the ocean basins. At timescales of  $10^3$  to  $10^5$  years

(e.g., over the Pleistocene or Quaternary periods), seawater volume is largely determined by the changing volume of ice sheets, and the associated redistribution of ice and water mass causes deformation of the earth surface and of the geoid. The former change is referred to as eustatic sea-level change, whereas the latter is referred to as glacial- and hydro-isostasy or geoidal change. At a timescale of  $10^2$  years (the timescale of global warming), the thermal expansion of seawater is the main factor that influences seawater volume, followed by melting of the ice sheets and ice caps (Bindoff et al., 2007); glacial- and hydro-isostasy or gravitational effect of water mass contribute a little to geographical variation in sea-level change at this timescale (Bamber et al., 2009).

Because sea level is a relative measure between the sea surface and land, vertical tectonic movements (i.e., uplift or submergence) also affect the relative position of the sea level; uplift and submergence of land result in a relative fall and rise, respectively.

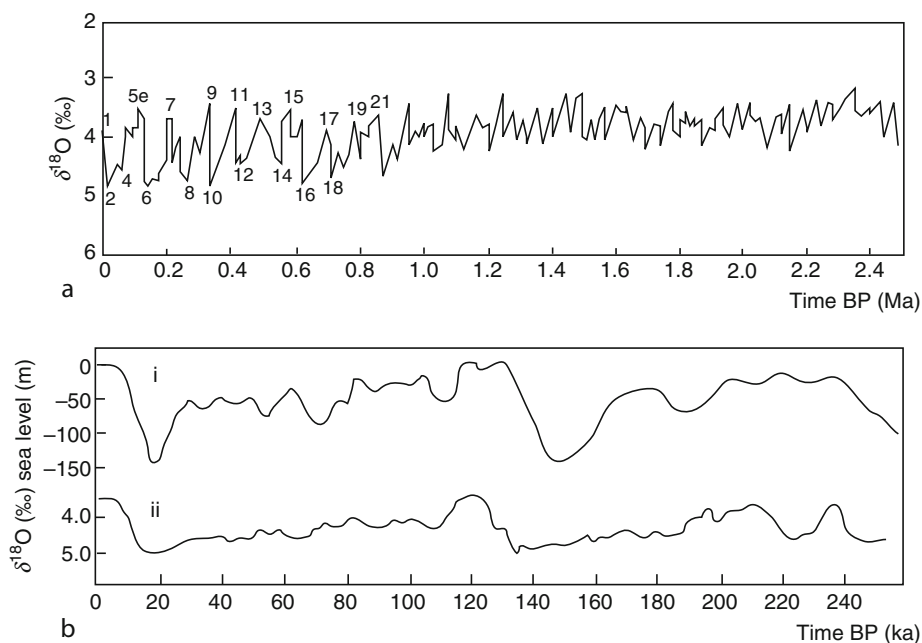
Coral reefs are formed below sea level (generally below the low level of spring tide); thus, sea level determines the available accommodation space in which reefs can grow. Because coral reefs are formed in shallow water, the most important factor in the growth of hermatypic corals with symbiotic algae is light, which diminishes with depth. Consequently, corals thrive at water depths from below low tide water level to 20–30 m. The formation of coral reefs is controlled mainly by sea level, while long-term reef growth and geomorphological development are controlled by sea level change and its rate.

## Pleistocene sea level change and its effects on coral reefs

### Pleistocene sealevel change

Since the Pleistocene period, around 2.6 million years ago, sea level has fluctuated with amplitudes of 120–140 m in response to changes in the volume of ice sheets. A record of sea level change over this period can be found in the oxygen isotope ratio ( $^{18}\text{O}/^{16}\text{O}$ ) of foraminifera preserved in deep-sea sediment cores (Figure 1). Depleted isotope ratios indicate the inflow of meltwater from ice, and thus, high sea level. In contrast, heavy isotope ratios indicate the storage of water in ice sheets on land, and thus, low sea level. The amplitude and oscillation cycles of sea level can be reconstructed from continuous records preserved in sediment cores. Another proxy for sea level change during the Late Pleistocene are raised coral reef terraces.

Synchronous changes in sea level and the climate in general suggest conspicuous cycles that, since 800 kyr ago, changed their lengths from 40 kyr (kyr = 1,000 years) to 100 kyr (Figure 1). These cycles match the cycles of the orbital oscillation of the earth (axial tilt and orbital eccentricity), which result in temporal and spatial variations in insolation and that trigger and maintain steady cycles of climate change. Since 800 kyr B.P., warm interglacial periods have occurred at 630, 330, 200, and 125 kyr ago (Lambeck et al., 2002). During each glacial cycle, sea level rose rapidly from a low of –100 to –140 m (relative to present) to levels similar to the present sea level as



**Sea Level Change and Its Effect on Reef Growth, Figure 1** Proxy records of Pleistocene climate and sea level change (from Figure 3.1 in Hopley et al., 2007). (a) Marine oxygen isotope record derived from benthic foraminifera of deep-sea core ODP677, Oxygen isotope stages marked in *italics*. (b) (i) Reconstruction of sea level derived from uplifted coral reef terraces, Huon Peninsula, Papua New Guinea; (ii) oxygen isotope record from benthic foraminifera.

climate warmed, and then oscillated at cycles of 40 and 20 kyr during a fallback to the low levels.

The last cycle, from 140 kyr ago to the present, is well recorded in deep-sea sediment cores and by coral reef terraces. The cycle is divided into six marine isotope stages (MIS-6 to MIS-1; Figure 2c). MIS-6 is the penultimate glacial maximum, during which time sea level dropped to  $-125$  m at 133 kyr ago. During the last interglacial period (MIS-5e), sea level rose rapidly to around the present level or up to 5 m higher. This was followed by a series of oscillations between relatively cold stadials (MIS-5d and -5b), when sea level was 40–60 m lower than that of the present day, and warm interstadials (MIS-5c and 5a), when sea level was 20–30 m lower than that of today (Lambeck et al., 2002).

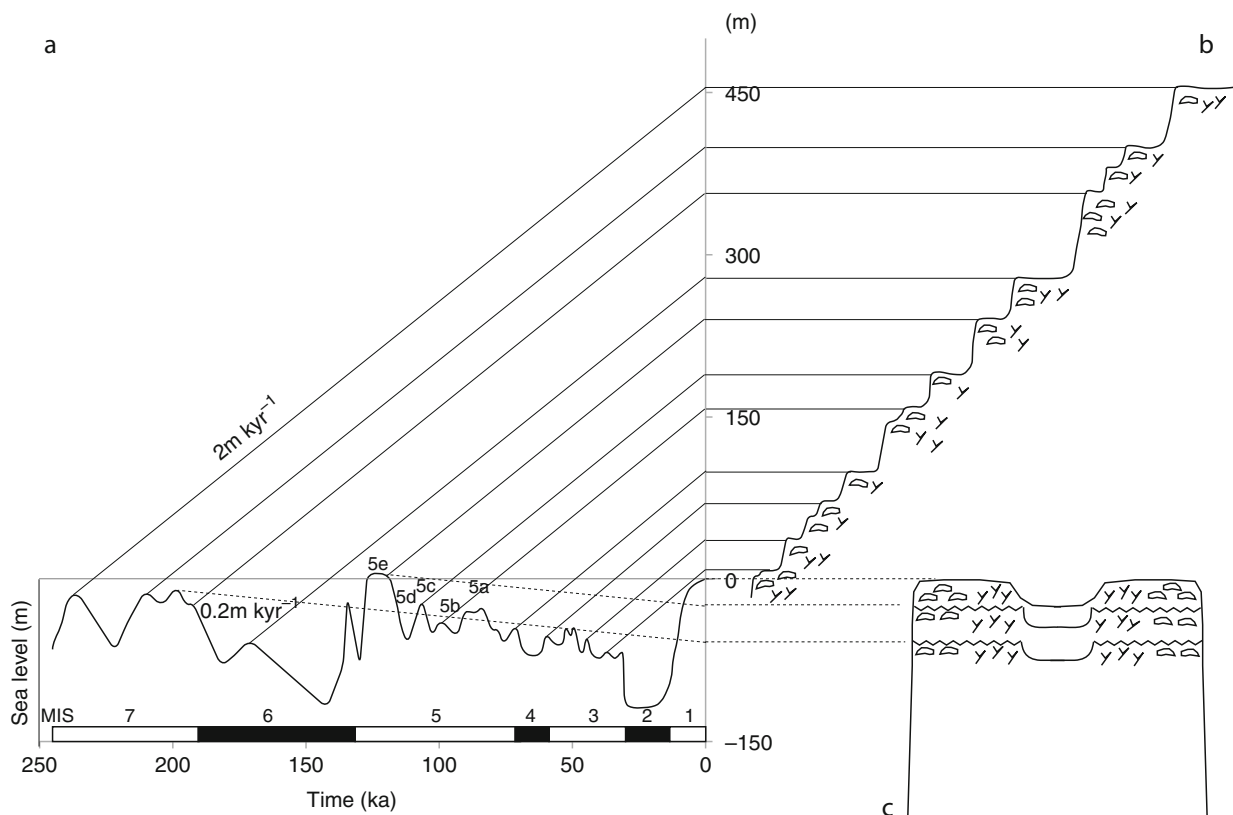
During MIS-4 and MIS-3, sea level fluctuated with an amplitude of 15 m between 40 and 70 m below the present level. During MIS-2, it dropped to a low of  $-125 \pm 5$  m during the Last Glacial Maximum.

### Effect of sea level change on coral reefs

During periods of low sea level (i.e., glacial times or cold stadials), coral reefs form on the edge of continental or island shelves at 100–140 m below the present sea level.

Moreover, the cold climate during these periods suppresses the formation of coral reefs, especially in subtropical regions. During periods of high sea level (i.e., interglacial times or warm interstadials), the rise in sea level provides space for reef formation on continental or island shelves, and reef formation is enhanced by the warm climate. Consequently, past coral reefs showed strong development during interglacial periods.

In tectonically active areas of continuous uplift, past coral reefs that formed during interglacial or interstadial periods have been uplifted above the present sea level (Huon Peninsula, New Guinea: Chappell, 1974; Chappell and Polach, 1991; Barbados: Mesolella et al., 1969, 1970; Vanuatu: Cabioch et al., 1998; Ryukyu Islands, Japan: Sasaki et al., 2004). Tectonic uplift generally occurs episodically: large seismic events typically occur at recurrence intervals of several hundred years with a displacement of up to several meters. However, at the timescale of sea level change ( $10^3$ – $10^4$  years), tectonic uplift can be regarded as temporally uniform. Thus, to use an analogy, tectonic uplift serves as a recording chart moving at constant speed, on which sea level is recorded like an oscillating pen-line on a chart (Mesolella et al., 1969). Therefore, regions with a high rate of tectonic uplift



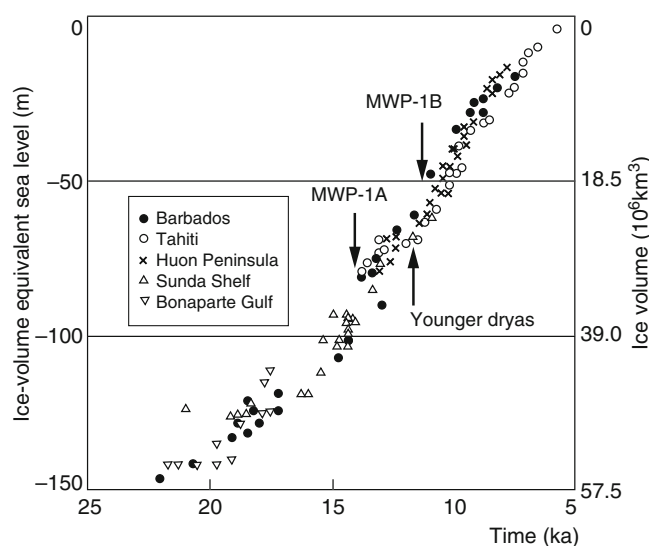
**Sea Level Change and Its Effect on Reef Growth, Figure 2** Model of the formation of coral reef terraces and an atoll by tectonic uplift and subsidence superimposed upon Pleistocene sea level change. (a) Sea level change for the last 240 kyr. (b) Formation of coral reef terraces with a constant uplift rate of  $2 \text{ m kyr}^{-1}$ . (c) Formation of an atoll with a constant subsidence rate of  $0.2 \text{ m kyr}^{-1}$ .



preserve coral reef terraces that formed during small-amplitude fluctuations in sea level. In other words, uplifted coral reef terraces provide an accurate record of sea level change, assuming a uniform rate of uplift (assumed to be  $2.0 \text{ m kyr}^{-1}$  in Figure 2b).

In tectonically stable areas, in contrast, coral reefs that form during interglacial periods are overprinted by reef formation during subsequent interglacials. Returning to the above analogy, it is as if the recording chart has stopped moving and the pen begins to record on the same part of the chart, thereby obscuring the earlier record. In such a case, only the most recently formed reef (i.e., that which formed during the current postglacial period, since 19 kyr ago; see the next section) is preserved to form the present coral reef landform (e.g., Mauritius: Montaggioni and Faure, 1997; Mayotte: Camoin et al., 1997; Great Barrier Reef, Australia: Marshall and Davies, 1982). In areas of ongoing submergence, coral reefs build upward upon preceding reefs.

The Huon Peninsula, New Guinea, contains well-preserved coral reef facies that formed during interglacial periods. The reef that formed during the Last Interglacial has been uplifted to 330 m above the present sea level; reefs that formed during other interstadial periods are also exposed upon the peninsula (Chappell, 1974). The raised coral reefs consist of shallow reef-crest facies, dominated by robust branching (or corymbose types) corals of *Acropora humilis* that overlie deeper fore-reef facies dominated by massive corals. This facies change, from deeper to shallower reefs, reflects the process of reef formation “catching up” to the higher sea levels during interglacial periods.



**Sea Level Change and Its Effect on Reef Growth,**  
**Figure 3** Post-glacial sea level change for the past 20 kyr (from Figure 5 in Lambeck et al., 2002). The sea level curve shows ice-volume equivalent one based on isostatically adjusted sea-level data from different localities. MWP-1A refers to the timing of the meltwater pulse at 14 kyr ago. At the Younger Dryas (YD) at 12 kyr ago, sea-level rise may have momentarily halted.

Oceanic atolls form in environments of submergence combined with oscillations in sea level. During glacial periods, when sea level is low, coral reefs are exposed to the air and eroded to form a karst surface, which modifies the original reef landform. During periods of high sea level, coral reefs become reestablished over the previously exposed surface. In such cases, seismic profiles across and drill cores in atolls reveal multiple reef layers separated by solution unconformities. The uppermost unconformities of this type are observed at  $-5$  to  $-20$  m below the present sea level, representing the erosion of coral reefs that formed at 125 kyr ago, during the last interglacial period (Dickinson, 2004). Figure 2c shows schematic profiles across an oceanic atoll with a subsidence rate of  $0.2 \text{ m kyr}^{-1}$ .

## Postglacial sea level change and its effects on coral reefs

### Postglacial sea level change

Sea level reached its lowest level of  $-125 \pm 5$  m below the present level from 30 to 19 kyr ago (MIS-2 or the Last Glacial Maximum). Subsequently, with melting of the ice sheets, sea level rose at an average rate of  $10 \text{ m kyr}^{-1}$  ( $10 \text{ mm year}^{-1}$ ), attaining the present level by 7 kyr ago (Figure 3). However, the rise was not temporally uniform: a period of rapid sea-level rise occurred at 14.5 kyr B.P. as a result of rapid decay of the ice sheets, resulting in a rate of sea-level rise of  $40 \text{ mm year}^{-1}$  over a period of 500 years (total rise in sea level: 15 m). This episode is termed meltwater pulse 1A (MWP-1A). Similar such episodes occurred at 19 and 11.5 kyr (MWP-1B) (Fairbanks, 1989). At 12 kyr, in contrast, sea-level rise was interrupted and remained constant for about 1,000 years, corresponding to a cold period named the Younger Dryas.

Sea level curves show spatial variations due to the variable glacial- and hydro-isostatic response of the earth to the melting of ice and redistribution of water. For small islands located far from the ice sheets (i.e., islands in far-field regions), the curve largely traces the change in ice volume, as described above. In the mid-Pacific, however, a 1–2 m high sea stand was observed during the mid-Holocene (Mitrovica and Peltier, 1991). At large islands and along the continental coast in far-field regions, this mid-Holocene high stand is evident as a hydro-isostatic effect. In the intermediate-field region, near the former ice sheets, the magnitude of the postglacial rise in sea level was much smaller than the equivalent rise in ice volume, because of submergence of the crust that had formed a bulge around the ice sheet. For example, in the Caribbean Sea, the amount of postglacial sea-level rise was 115 m in Barbados (Fairbanks, 1989), and sea level has risen continuously to the present level at smaller average rates. The geographic differences between the Indo-Pacific Oceans and Caribbean Sea have resulted in contrasting histories of sea level change. In the Western Indian Ocean, sea level has never been higher than that of the present (Camoin et al., 1997, 2004).

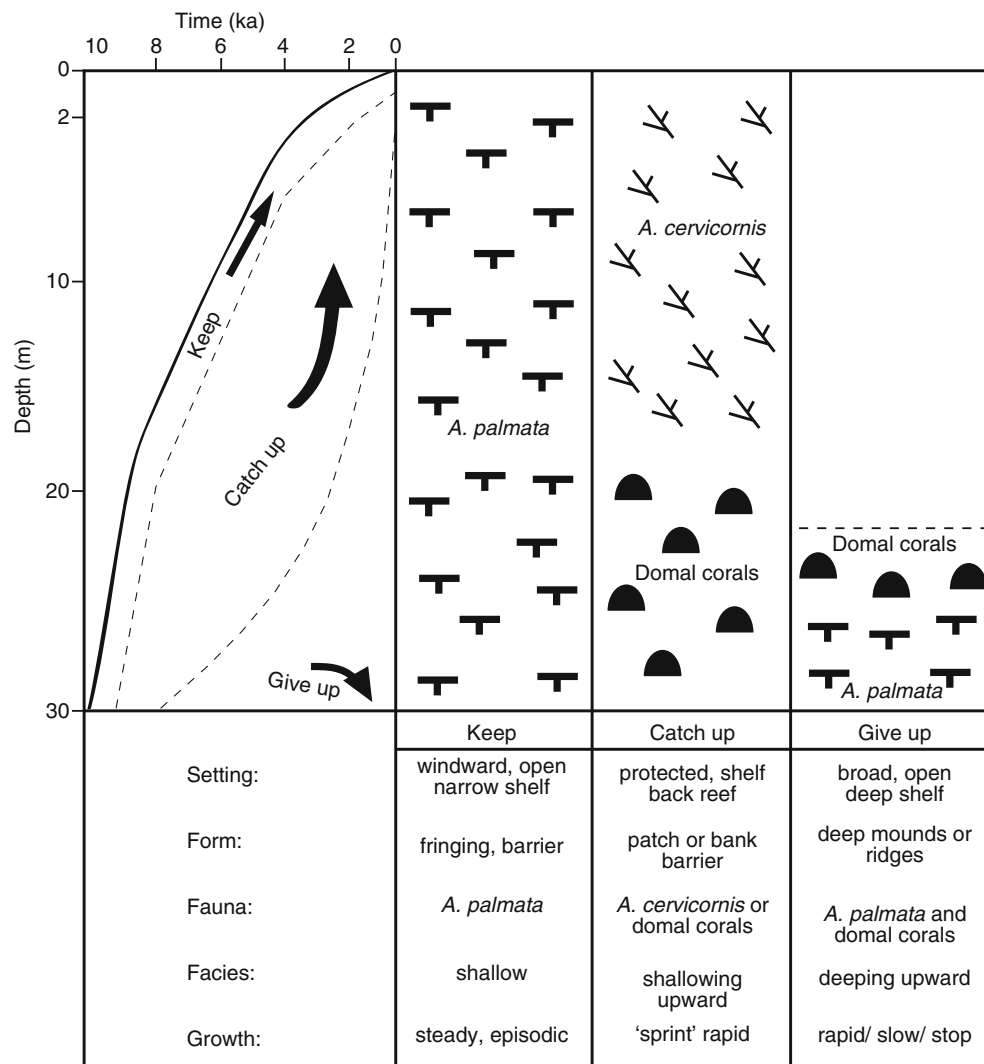
### Effect of postglacial sea level change on coral reefs

Coral reefs grow upward to fill the available water space created by a rise in sea level. The different patterns of reef growth in response to postglacial change in sea level can be classified into keep-up, catch-up, and give-up styles (Davies et al., 1985; Neumann and Macintyre, 1985).

Keep-up reefs grow at a rate equal to sea level rise, thereby maintaining the upper reef surface close to the sea surface throughout its growth (Figure 4). Keep-up reefs consist entirely of shallow-water corals throughout their growth. In each case, a robust-branching (corymbose) form of *Acropora* is the main reef builder: *A. palmata* in the Caribbean Sea (Lighty et al., 1982) and *A. humilis*, *A. robusta*, and *A. danai* in Indo-Pacific reefs (Fairbanks, 1989; Bard et al., 1996; Camoin et al., 1997; Montaggioni et al., 1997). These corals grow in

water depths of less than 6 m (Lighty et al., 1982; Cabioch et al., 1999), with a vertical accumulation rate of less than  $6 \text{ m kyr}^{-1}$ .

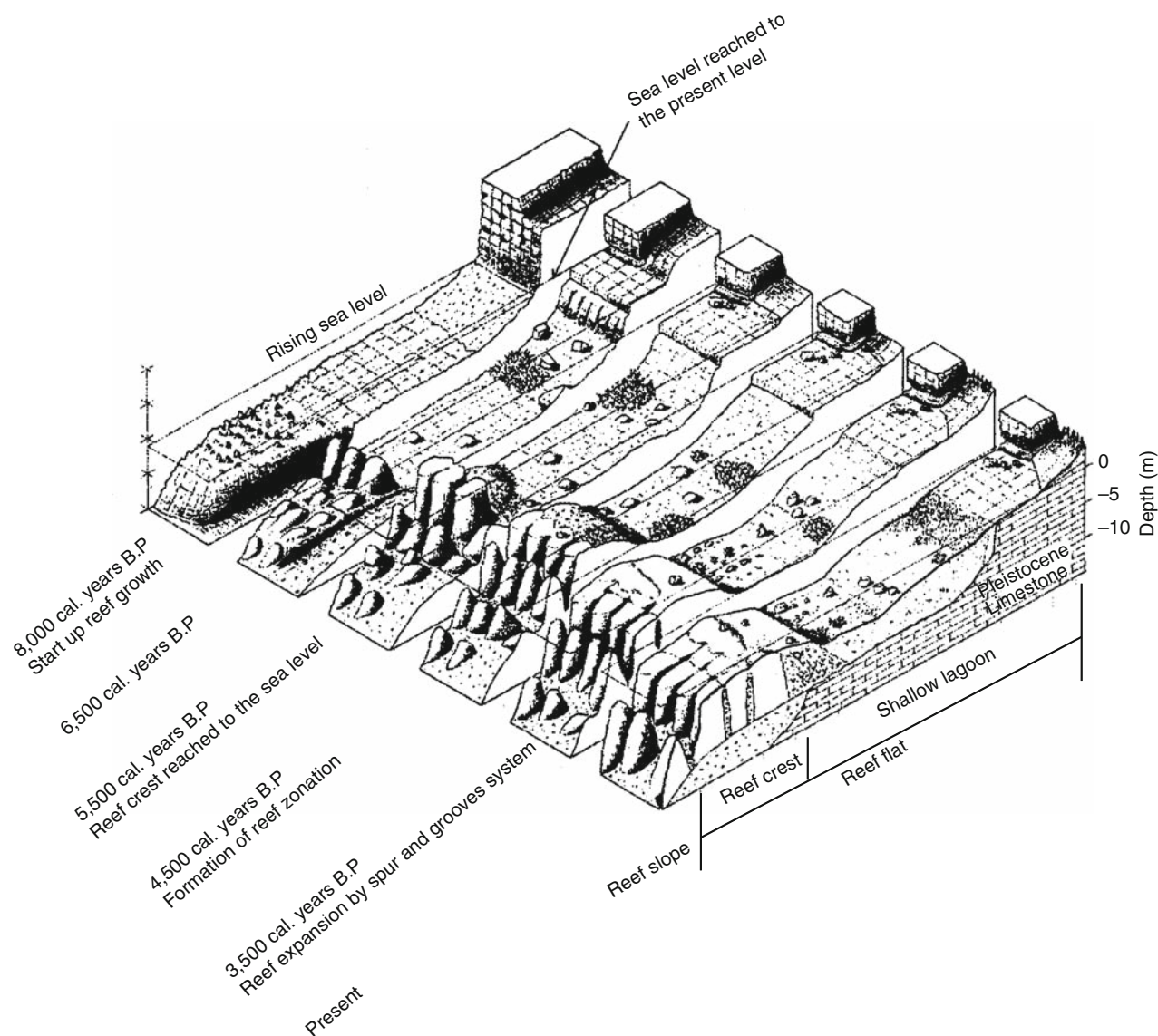
Catch-up reefs begin to grow from a relatively deep site, finally catching up with sea level before or after sea level has stabilized. Catch-up reefs consist of shallow-water facies (robust-branching corals) underlain by deeper-water facies that generally consist of encrusting corals (e.g., *Echinopora gemmacea*, *Platygyra daedalea*, *Pachyseris rugosa*, and *Leptoria irregularis*), and bioclastic sand and gravel. There is little biogeographical variation in the species of robust-branching corals. In the Indian Ocean and Western and Central Pacific, the robust-branching corals in catch-up reefs consist of *A. digitifera*, *A. hyacinthus*, *A. cytherea*, *Pocillopora verrucosa*, *Goniastrea retiformis*, and *Favia stelligera*



**Sea Level Change and Its Effect on Reef Growth, Figure 4** Styles of reef growth in response to post-glacial sea level change (Based on Figure 3 in Neumann and Macintyre, 1985).

(e.g., Montaggioni and Faure, 1997; Cabioch et al., 1999; Kayanne et al., 2002; Hongo and Kayanne, 2009). In the East Pacific and Hawaiian Islands, such corals consist of *P. damicornis*, *P. meandrina*, and *Porites compressa* (Easton and Olson, 1976; Cortés et al., 1994; Grigg, 1998). The vertical accumulation rate of the deeper facies sometimes exceeds  $10 \text{ m kyr}^{-1}$ , reaching up to  $20 \text{ m kyr}^{-1}$ , but the rate decreases as the reef catches up with the sea surface and the corals change to shallow-facies species (Kayanne, 1992). Vertical accretion of the reef ceases once it has caught up with the sea surface, thereafter being replaced by lateral growth. Many coral reefs have kept pace with rising sea level for the past 11 kyr (Davies et al., 1985; Montaggioni, 1988).

Give-up reefs are those unable to catch up the rising sea level, eventually becoming deeply submerged and dying off. Give-up reefs are a common feature of many insular shelves in the eastern Caribbean (Macintyre, 1972) and the Great Barrier Reef (Harris and Davies, 1989). Barbados, in the Caribbean, is rimmed by three relict reefs consisting of *A. palmata* at  $-80$ ,  $-40$ , and  $-10 \text{ m}$  below the present sea level; these reefs yield ages of 11–18, 10–11, and 6–9 kyr, respectively (Fairbanks, 1989). A complex ridge system occurs along the shelf edge of the St. Croix. A shallow-water *A. palmata* reef flourished on the shelf edge off south coast of St. Croix 9 kyr ago, but eventually succumbed to stress caused by rising sea level (Macintyre, 1988).



**Sea Level Change and Its Effect on Reef Growth, Figure 5** Holocene history of reef formation and reef zonation. Based on Figure 1 in Kan (2007) with permission from Department of Geography, Tokyo Metropolitan University.



After the reef submerged by rapid rise in sea level, the new reef was formed at the landward position from the submerged reef (back-stepping). On the other hand, in tectonically active areas, as the reef uplifted episodically (in general accompanying with seismic activity), the new reef was formed seaward of the raised reef, and progradation occurred episodically rather than gradually (Kayanne et al., 1993).

A distinct reef zonation develops following the stabilization of sea level (Figure 5). Corals are characterized by a variety of growth forms whose distribution is related to gradients in environmental factors such as light, sediment, and wave energy. Wave energy is especially important in this regard (Chappell, 1980; Yamano et al., 2003; Hongo and Kayanne, 2009). For example, robust-branching corals are characteristic of settings with high wave energy. In the Caribbean, this corresponds to a zone of *A. palmata* (Lighty et al., 1982); in the Indo-Pacific: *A. humilis*, *A. robusta*, *A. digitifera*, and *P. verrucosa* (Cabioch et al., 1999). In settings with very high wave energy, corals are replaced by calcareous algae (Geister, 1977; Grossman and Fletcher, 2004). Indeed, an algal ridge is a prominent feature of many Indo-Pacific and Caribbean. Arborescent corals (e.g., *A. muricata*, *A. intermedia*, and *A. cervicornis*) grow in relatively sheltered reefs, and foliaceous and encrusting corals (e.g., *E. lamellose*, *P. rugosa*, and *L. irregularis*) are common in settings with low wave energy.

Reef islands are common features of atolls (Stoddart, 1969). In areas with frequent storms, reef islands generally contain gravel deposits on the windward side of the atoll. In storm-free areas, in contrast, gravels are not major component, and sand cays are developed on the atoll. It is likely that reef islands show temporally variable rates of accretion in response to environmental change (e.g., Holocene sea level change and ocean conditions). For example, sea-level fall over a period of 2,000–4,000 years may be necessary for a reef island in the Pacific (Buddemeier et al., 1975; Woodroffe et al., 1990; McLean and Woodroffe, 1994). Although reef islands are from areas in which sea level has fallen, similar reef islands are found in the Caribbean and Indian Ocean, where sea level rose or was stable during the formation of reef islands (Woodroffe et al., 1999; Kench et al., 2005).

## Conclusion

At timescales greater than  $10^3$  years, sea level change is the primary factor controlling the formation of coral reefs. Accordingly, coral reefs represent the most effective proxy in reconstructing the history of sea level change. For example, the most precise history of sea level change during the Late Pleistocene and postglacial period is attained from analyses of coral reef terraces and drill core recovered from modern reefs. However, such an approach is susceptible to circular reasoning in terms of assessing the response of coral reefs to sea level change, which itself is reconstructed based on the formation process of coral

reefs. To overcome this problem, it is important to obtain independent signatures of sea level change (e.g., peat; Toscano and Macintyre, 2003) and to evaluate the reliability of specific corals for sea level proxies.

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[Solution Unconformities](#)

## SEAGRASSES

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## Definitions

Seagrasses are monocotyledon flowering plants adapted to marine environments.

Seagrass beds or meadows are marine communities comprising seagrass species that provide habitat for many other organisms.

## Introduction

Seagrasses are the only botanical species whose ancestors recolonized the sea. This unusual group of vascular plants is generally defined as a diverse assemblage of angiosperm, monocotyledon plants found in brackish or more usually in marine waters of relatively shallow tropical and temperate regions of the world. These submerged flowering organisms complete their entire life cycle underwater producing oxygen as they photosynthesize radiant energy. Seagrasses are normally rooted in thick, often vast, productive beds or meadows. As salt-water plants, they influence the physical, chemical, and geological processes affecting coastal environments in which they live by filtering waters and dissipating wave energy. Seagrasses also anchor sediments and thus provide protection from erosion. In addition, they provide habitats and food resources for many invertebrates, fish, and avian species, as well as a few reptiles and mammals, including some endangered marine species. Unfortunately, today many seagrass beds have been severely degraded due to a variety of human activities. Protection of these communities is essential for the preservation of many marine species (Figure 1).

## Seagrass biology

Seagrass species have apparently evolved from dissimilar groups of freshwater plants; indeed, some seagrass species are closer in their evolutionary relationship to certain freshwater plants than they are to other seagrasses (Waycott et al., 2006). Although some water plant species can be found in marine habitats with low to moderate salinity, the assemblage of plant species defined as seagrasses occur only in oceanic water bodies with high salinity. These species do not require contact with the atmosphere, and their sexual reproductive cycle, including flowering and pollination, is completed under water. Particular adaptations of seagrasses to a life submerged in saltwater include an efficient ability to incorporate inorganic carbon from ocean water. They are able to obtain nutrients required for growth in some cases by direct uptake through their roots (similar to the process used by terrestrial plants), or in many situations, through their leaves from the water column itself. However, because sea floor sediment is typically deficient or devoid of oxygen, the underground parts of seagrass plants commonly obtain oxygen via their leaves by way of a system of air-filled channels that develop within their living tissue. Another important adaptation common to most seagrasses is their strap-like leaves (den Hartog, 1970), which allows these plants to flourish in aquatic environments that are heavily affected by the flows of tides and waves. Among seagrasses, pollen dispersal to female flowers,

typically aided by wind or insects in land plants, occurs via water currents (Borum et al., 2004).

## Seagrass research

Early research involving seagrasses focused on taxonomic comparisons of their superficial morphology with that of other plant groups and only relatively little attention was directed toward other botanical or human use aspects of these plants. The study of additional scientific and resource management aspects of seagrasses accelerated in the second half of the twentieth century; one publication in the late 1970s (Bridges et al., 1978) cited more than 1400 references from sources worldwide, and many, more recent studies of seagrasses have been undertaken during the past few decades (e.g., see Green and Short, 2003; Borum et al., 2004; Larkan et al., 2006; Heck et al., 2008).

## Seagrass taxonomy

Seagrasses are not true species of grass which all belong to the family Poaceae. In fact, seagrasses as a whole are best referred to as an ecological group rather than a taxonomic group. There is still no officially recognized classification system that completely describes the recorded genera of "true seagrasses." This situation can be explained by the polyphyletic nature of seagrasses, as well as the lengthy debate over placement of the individual genera into respective families and the lack of an accepted scientific definition of "seagrass." Although the quantity and biological classification of seagrass species is still disputed, it has generally been assumed that there are approximately 50–60 species of these marine flowering plants (Duarte, 2008; Hogarth, 2007; Hughes et al., 2009), belonging to 12 genera in four families. These include species in the following genera and families: *Posidonia* in the family Posidoniaceae; *Zostera*, *Heterozostera*, and *Phyllospadix* in the family Zosteraceae; *Enhalus*, *Halophila*, and *Thalassia* in the family Hydrocharitaceae; and *Amphibolis*, *Cymodocea*, *Halodule*, *Syringodium*, and *Thalassodendron* in the family Cymodoceaceae (according to Duarte (2008), over 50% of the seagrass species belong to *Halophila*, *Zostera*, and *Posidonia*; see Kuo and den Hartog, 2001 for short descriptions of all seagrass species recorded as of 2006). Other, recent phylogenetic research suggests that seagrass species can be further divided into six families: Cymodoceaceae, Hydrocharitaceae, Posidoniaceae, Ruppiaceae, Zannichelliaceae, and Zosteraceae (Waycott et al., 2006). However, even this taxonomic perspective is debatable since species belonging to the genera of *Ruppia* and *Zanichella* are able to complete their life cycles beyond marine waters (Larkum et al., 2006). Furthermore, some recent authors continue to refer to Potamogetonaceae as one of the seagrass families (e.g., Allen, 2003; Hogarth, 2007; Duarte, 2008).

## Seagrass biogeography

Seagrass species vary in the size of their leaves from more than 4 m long, as occurs in the strap-like blades of *Zostera caulescens* (eelgrass) in the Sea of Japan, to only 2–3 cm



in the rounded blades of *Halophila decipiens* (sea vine) in relatively deep tropical marine areas adjacent to Brazil. Seagrasses of one or sometimes multiple species often form extensive beds or meadows over shallow, unconsolidated sediments on all continental shelves except those of Antarctica, as well as on inshore environments of many oceanic islands of the world. For example, huge underwater seagrass beds occur along sections of the coasts of Australia, Alaska, southern Europe, India, east Africa, the islands of the Caribbean, and other places around the globe. The maximum water depth in which these salt-water plants are known to occur is ~90 m (Duarte, 1991). They can be found in both temperate and tropical marine environments, frequently growing near to and associated environmentally with coral reefs, mangroves, salt marshes, bivalve reefs, and other saline aquatic habitats. Seagrass beds can be either monospecific, comprising only a single species, such as *Zostera marina* in parts of the North Atlantic, or multispecific, where various species coexist, such as in tropical marine environments like the Philippines where up to 13 species are known to occur. The highest diversity of seagrasses in the world exists in Australia, which harbors over half of the world's species and contains the most widespread seagrass beds found anywhere (Butler and Jernakoff, 1999). New records of seagrasses are still being established, and in at least one case these records have expanded the known biogeographical distribution of some species. For example, until recently, the only seagrass species recorded in the Hawaiian Islands was the endemic *Halophila hawaiiiana* (Doty and Stone, 1966); however, we now know that a close relative, the very widespread seagrass species *Halophila decipiens*, also occurs in the Hawaiian Islands, where it was first recorded from Midway Atoll, and is now known from at least three locations spanning the archipelago (McDermid et al., 2002).

### The geomorphological role of seagrasses

Seagrasses play a role in helping create their own habitat, and thus they have been referred to as “ecosystem engineers” (Wright and Jones, 2006; Coleman and Williams, 2002). For example, their leaves reduce the speed of ocean currents which enhances sedimentary processes, and the roots and rhizome of seagrasses aid in the stabilization of the seabed; they literally hold or bond reefs together. In addition, seagrass beds improve water quality by stabilizing loose sediment and filtering some pollutants out of the water column. If seagrass beds were not in place, widespread marine areas in the world would have environments with unstable, shifting sand and mud. A recent modeling study by the United Nations Environmental Program, based on data collected from the effects of the huge 2004 Indian Ocean Tsunami, suggests that seagrasses provide the significant beneficial effect of absorbing wave energy and can thus reduce physical and biological damage from such a potentially devastating natural hazard (Chatenoux and Peduzzi, 2005).

### The ecological roles of seagrasses

Seagrasses provide a large number of vital ecological services to the marine habitats in which they are “foundation species” (e.g., Costanza et al., 1997; Hemminga and Duarte, 2000; Conservation International, 2008). Their significance for associated species is based primarily on the protective cover they provide by means of their three-dimensional configuration in the water column, as well as their extremely high rate of primary production (e.g., Virnstein, 1982; Phillips, 1992; Heck et al., 2008). Consequently, seagrasses supply inshore habitat with many ecosystem goods and services, such as nurseries for finfish, shellfish, and crustaceans; protection of biota from wave damage; production of oxygen; and shelter against coastal erosion. Generally, seagrass beds can be characterized as among the most productive natural communities in the world serving as major suppliers to the marine food web. Thousands of plants, animals, and other organisms live among the seagrasses in a multifaceted and delicate ecological environment. For example, sea turtles and sea cows (dugong and manatees) graze upon seagrass species, and numerous kinds of worms, snails, shrimps, crabs, and small fish live their whole lives within seagrass beds. In addition, many marine fish important to fishermen depend upon seagrass communities during some periods of their lives, and bigger fish and seabirds also come to these beds to eat the smaller animals. Although the role of seagrass (as well as mangrove) habitats as nurseries for coral reef fish species has long been debated, a study of the use of seagrass habitats by juvenile coral reef fish using visual census surveys at four islands along the East African coast of Tanzania and at the island of Grande Comoros in the Comoros archipelago indicates that areas with seagrass beds had a positive influence on the adult concentration of several reef fish species on adjoining coral reefs (Dorenbosch et al., 2005:63).

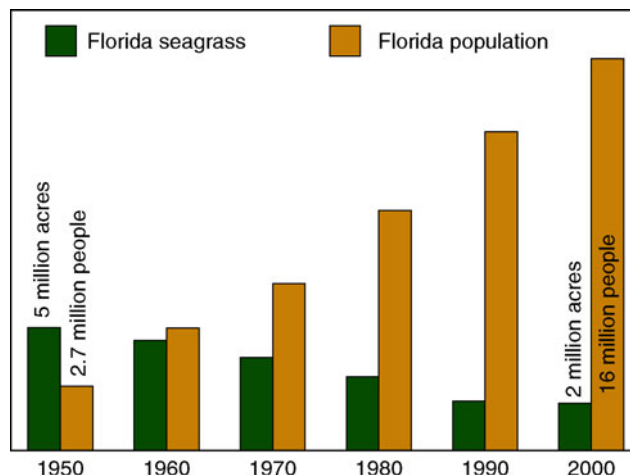
### Conservation issues affecting seagrasses

Seagrass beds can extend into deep waters, and those that still cover large areas today are typical of marine coastal environments that have not suffered from significant human impact. Because of the amount of light that seagrasses require, the depths in which they can survive are limited by water clarity, and because these marine plant species are generally perennial organisms, they develop over time into integrated, often highly diverse, biological communities. Therefore, seagrasses are prime indicators of the degree of anthropogenic disturbance in marine habitats, and thus they are useful for periodic ecological observation and the implementation of effective management policies. Even though a number of scientists and some concerned citizens recognize that healthy seagrass beds are of great value both ecologically and economically, a large number of their habitats in many regions of the world have been totally ruined or are being degraded rapidly by a multitude of human activities in the form of nutrient loading, siltation, and mechanical



**Seagrasses, Figure 1** *Enhalus acoroides* (L.f.) Royle [family: Hydrocharitaceae] shown here growing in the marine environment of Yap where it is one of seven seagrass species recorded from this area in Micronesia (photo: Mark D. Merlin).

disturbance (e.g., Short, 1987; Shepard et al., 1989; Short and Wyllie-Escheverria, 1996; Cardoso et al., 2004; Orth et al., 2006). Runoff of nutrients and sediments resulting from human activities on land are most likely the main overall threat to the existence and health of seagrass beds worldwide. Because of the relatively high light requirements of seagrass species, they are quite susceptible to the effects of nutrient and sediment loading on water clarity. Seagrass beds are also damaged directly by inappropriate boating activities, dredge-and-fill activities, and harmful commercial fishing practices. For example, the seagrass beds of Florida's coastal areas were reduced in aerial extent by about 60%, from approximately 5 million acres to 2 million acres, during the second half of the twentieth century (Figure 2), mainly by dredge-and-fill projects and reduced water quality (Florida Fish and Wildlife Conservation Commission, 2007). Global climate change that can result in rising sea level and the production of more frequent severe storms could and may already be having



**Seagrasses, Figure 2** Loss of seagrasses in Florida (1950–2000) is shown in relationship to the increasing human population in the State of Florida. Source: Florida Fish and Wildlife Conservation Commission. 2007. *Florida's Seagrasses*. Florida St. Petersburg, FL: Fish and Wildlife Research Institute, a Public Brochure.

impact on the range and vigor of seagrasses (Short and Neckles, 1999). Furthermore, seagrasses are the main food or are associated in other ways with a number of threatened and endangered species (e.g., see Hughes et al., 2009; Preen and Marsh, 1995); these include species such as the Green sea turtle (*Chelonia mydas*), fan mussel (*Pinna nobilis*), dwarf seahorse (*Hippocampus zosterae*), and dugong (*Dugong dugon*). Indeed, green sea turtles as well as dugongs and manatees (*Trichechus* spp.) are recognized as appealing species of significant public interest, and therefore the reduction and degradation of their necessary seagrass environment is a tragedy for these and many other species. Unfortunately, seagrasses worldwide are generally receiving modest protection even though there are numerous pressures on their various coastal habitats (Green and Short, 2003). Scientists agree that there is a strong need for competent monitoring and management strategies for many, if not most, seagrass species and their homes on coral reefs and other environments (e.g., see Duarte, 2002; Green and Short, 2003; Borum et al., 2004; Hughes et al., 2009). Furthermore, a significant increase in public awareness through communication and education regarding the important ecological and economic roles of seagrass communities is strongly needed to enlighten and stimulate effective management of these crucial coastal seagrass beds and the species that inhabit them (Duarte et al., 2008).

## Summary

Seagrasses are unusual, important, and underappreciated species that inhabit coral reefs and many other marine habitats. Extensive, naturally occurring seagrass beds or meadows provide key ecological and economic resources



for many coastal ecosystems worldwide. Even though there are still widespread seagrass beds on all of the world's continents except Antarctica, seagrass beds and the species they harbor have been reduced in size or completely destroyed in many areas. Human population continues to expand and become increasingly urbanized, with more and more people residing disproportionately in the world's coastal regions. Consequently, an increase in scientific study, effective resource management, and a major rise in public awareness of the environmental importance of seagrasses as coastal resources and vital habitats are more important than ever.

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## Cross-references

Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity  
 Climate Change: Impact On Coral Reef Coasts  
 Great Barrier Reef Committee  
 Midway Atoll (Hawaiian Archipelago)  
 Nutrient Pollution/Eutrophication  
 Pacific Coral Reefs: An Introduction  
 Reef Flats  
 Reef Front Wave Energy  
 Tsunami

## SEA-LEVEL INDICATORS

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### Definition

*Sea level* is the local height of the ocean's surface, usually measured to a datum referenced to a tidal position established from a record in which high-frequency motions such as wind waves and periodic changes (e.g., due to the tides) have been averaged out. Local sea level fluctuates regularly with tides and irregularly in response to factors including wind and currents, water temperatures and salinities, and atmospheric pressure.

*Relative sea level* is the elevation of the sea surface relative to the land at a given location. Global or eustatic sea-level fluctuations occur as the volume of water in the earth's oceans changes when ice caps and glaciers grow or melt, or as large-scale changes in the configuration of ocean basins and continental margins occur through plate tectonics. There are also regional and local isostatic processes that produce spatially different patterns of relative sea-level change, including thermal expansion of surface waters, changes in meltwater load, crustal adjustment of areas directly or indirectly affected by ice on- and off-loading (see *Glacio-Hydro Isostasy*), coastal uplift or subsidence due to tectonic processes (see *Earthquakes and Emergence or Submergence of Coral Reefs*), and subsidence due to aquifer depletion or sediment compaction.

*Sea-level indicators* are used to determine relative sea-level changes at a location. Locating a sea-level indicator and determining its age and elevation relative to its modern counterpart can establish relative sea-level change. Sea-level indicators on coral reefs include a range of biological, geomorphological, sedimentological, and chemical features that provide information on the position of the sea surface at the time that they lived or were formed. They usually comprise features with a known relationship to a tidal position or datum.

### Introduction

Coral reefs are best developed in warm, clear tropical waters less than 30–50 m deep, where photosymbiotic organisms can access abundant energy provided by the

tropical sun (Falkowski et al., 1990) (see *Corals – Environmental Controls on Growth*). The restriction of vigorous reef growth to shallow depths is well known, and at the broadest level coral reefs at elevations and depths where they no longer survive have been used to determine larger longer-term sea-level changes, like those of the Quaternary (Bloom et al., 1974; Chappell, 1974; Cabioch and Ayliffe, 2001) (see *Emerged Reefs; Barbados; Huon Peninsula, P. N. G.; Submerged Reefs*).

A reef's shape can suggest an approximate depth, allowing the sea-level signal derived from whole reefs to be refined further (Adey, 1978). However, the most precise estimates of past sea-level position are established from the vertical zonation with respect to sea level of: (a) the range of plants or animals that live on and construct coral reefs and (b) the range of physical and chemical processes that may leave datable sedimentary or erosional signatures (Davies and Montaggioni, 1985; Hopley, 1986b) (see *Geomorphic Zonation*). Accordingly, coral reefs are recognized as valuable repositories of sea-level information, and sea-level studies from coral reefs have flourished in recent decades.

### Key attributes of useful sea-level indicators

Sea-level indicators on coral reefs are either *finite* (syn: *diagnostic* or *indicative*) or *directional*. Finite sea-level indicators have a definite relationship with the sea surface, whereas directional sea-level indicators only document whether sea level was above or below the indicator at the time of its formation (Chappell et al., 1983; Davies and Montaggioni, 1985). The growth or formation of finite sea-level indicators is usually restricted to a specific intertidal, shallow subtidal, or possibly peritidal depth range, and a quantitative relationship between the sea surface and the indicator can be established. This relationship is referred to as the "indicative meaning," which for a particular indicator in its local environment may have an elevational range quantified and reduced to a datum expressed relative to a tide level (e.g., mean low water springs (MLWS)) with an associated error range (van de Plassche, 1986). Finite indicators are normally constrained within a narrow (<2 m) depth range, and are usually formed within 5 m of the sea surface (Davies and Montaggioni, 1985). Finite indicators are preferred for high-resolution sea-level studies, but are rarely formed during rapid transgressions or regressions (see *Postglacial Transgression*).

Excellent reviews of sea-level indicators are provided by Davies and Montaggioni (1985), van der Plassche (1986), and Pirazzoli (1991). These and other studies conclude that the key attributes of useful sea-level indicators are:

1. A narrow vertical depth range
2. A reproducible elevation
3. Good geological preservation
4. Capacity to be accurately dated

The major sea-level indicators used to establish sea-level histories on coral reefs satisfy the above criteria, and are described below.

### Main sea-level indicators on reefs

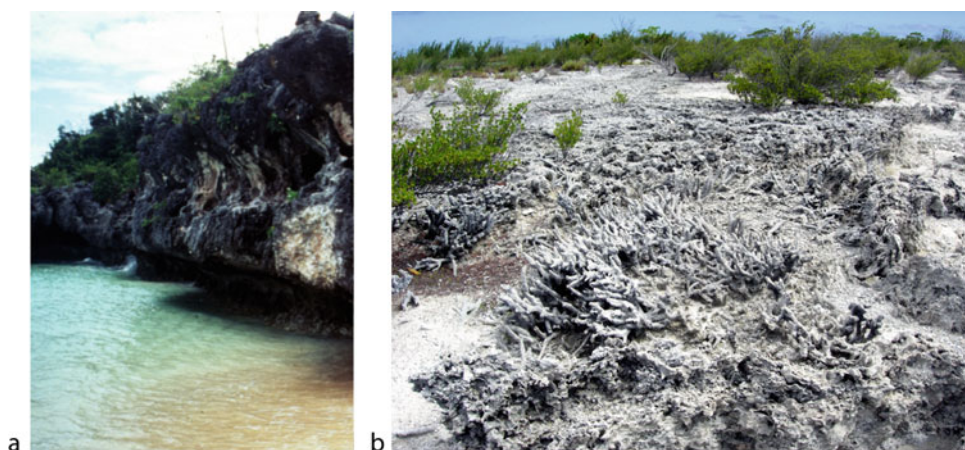
#### Coral reefs and corals

Sea level constrains coral reef growth and significantly influences coral reef morphology; continued upward growth is limited by emergence, and the depth below sea level at which reef growth can occur is limited by light – calcification by reef-building organisms is most efficient in the upper euphotic zone, which is normally within 50 m of the surface (Falkowski et al., 1990) (see *Corals – Environmental Controls on Growth*). Although individual corals may survive in deeper waters, they rarely develop reefs because photosynthetically active radiation is limited, reducing calcium carbonate production and accumulation to below rates of removal. Actively growing coral reefs are thus confined to a narrow (~50 m) depth window near the sea surface that makes them excellent gross indicators of sea-level position. The upper 30 m, in which most of the world's coral reefs grow, represents <1% of the mean 3,729 m depth of the world's oceans (Hopley et al., 2007).

Coral and coral reef cores provide many sea-level data. With few exceptions (identified below), they must be considered relatively imprecise directional sea-level indicators as the depth at which a coral grew can rarely be precisely determined, and thus the indicative range may be >30 m. However, corals and many other reef materials have good preservation potential and can be accurately dated using radiocarbon and uranium-series methods (see *Radiocarbon ( $^{14}\text{C}$ ): Dating and Corals; Uranium Series Dating*). As a result, sea-level data from coral reefs generally have relatively large elevation but small age-error terms.

Coral reefs have made a particularly important contribution to the knowledge of Quaternary sea-level

fluctuations. Dating of emergent reefs at relatively stable mid-plate oceanic islands (e.g., Oahu, Hawaii) and at stable continental margins (e.g., Western Australia) showed that sea level during the last interglacial (LIG) was ~6 m above present (Stirling et al., 1995) (see *Emerged Reefs*). Recent work from other Caribbean and Indo-Pacific reefs suggests the LIG peak was 2–10 m higher than at present (Chen et al., 1991; Israelson and Wohlfarth, 1999). Relict coral reefs drowned by rapidly rising postglacial sea levels are also known from several areas (“give-up” reefs of Neumann and Macintyre (1985); see *Reef Classification, Response to Sea Level Rise*) that provide valuable sea-level data. For example, drowned reefs with shallow-water features have been described and dated off the west coast of Barbados (e.g., Macintyre et al., 1991) and southeast Florida (Lighty et al., 1978) in the Atlantic (see *Barbados*), and similar features have been described on the Great Barrier Reef (GBR) shelf edge (Harris and Davies, 1989; Hopley et al., 1997). The shallow-water features and facies on many of these reefs have been interpreted as evidence of relatively slowly rising or briefly stable sea-level periods during the postglacial transgression (see *Postglacial Transgression*), with the termination of reef growth attributed to rapid submergence associated with meltwater pulses (see *Meltwater Pulses*) or water quality or temperature constraints (Macintyre, 1972; Adey et al., 1977; Lighty et al., 1978; Macintyre et al., 1991) (see *Submerged Reefs*). Ironically, the best records of past sea-level change are not preserved in tectonically stable areas because evidence can be eroded, reworked, or buried by subsequent sea-level oscillations. Emergent reefs formed as fringing reefs (see *Fringing Reefs*; Figure 1a) on rapidly uplifting coasts yield the best evidence for Quaternary sea-level changes, as whole reef geometry, biological and geomorphological zonation (see *Geomorphic Zonation*), and sediment facies can be observed and interpreted for accurate paleo-sea-level



**Sea-level Indicators, Figure 1** (a) Uplifted reef terrace, Sohona, Bouganville, Papua New Guinea; (b) emergent mid-Holocene reef at Kirimati, Kiribati, showing intact in situ *Acropora* still in growth position, approximately 1 m above modern equivalents.

determination (Sasaki et al., 2004). Recent improvements in technology have greatly enhanced access to and detailed observations of submerged reefs in areas of tectonic subsidence (Faichney et al., 2009) and deep submarine slopes (see *AuVs (RoVs)*; *Swathe Mapping*). These hitherto largely inaccessible reefs will no doubt give up valuable sea-level information in future years.

Emergent reefs provide access to a range of dateable materials, some of which may be cross-checked with other evidence to improve the accuracy of reef growth and sea-level chronologies (Figure 1b). Fossil corals from reef terraces have been radiometrically dated and compared with the deep-sea record of ice-volume changes to deduce large-scale sea-level change, but the details of the reef terrace and deep-sea sea-level interpretations are less perfectly accordant beyond the limit of radiocarbon dating (e.g., ~40,000 years; Cabioch and Ayliffe, 2001).

Relative sea level at any location is a function of vertical movements of the land and changes in the absolute elevation of the sea. Where tectonic uplift and sea-level rise rates are comparable, *relative* sea level stability may be encountered and reef flats may form. The same eustatic sea-level change will produce dissimilar reef terrace sequences in areas with different tectonic histories. However, if long-term rates of uplift or subsidence are known and reef terraces age can be established, the sea level at the time of reef formation can be calculated. The coordinated analysis of sea-level histories reconstructed from reef terraces at locations with different tectonic heritages has enormously progressed knowledge of the amplitude and timing of Quaternary sea levels.

Where in situ coral immediately overlies an unconformity, reef growth over transgressive surfaces is indicated by paleosols, diagenetic alterations (see *Diagenesis*), and calcrete stringers (see *Calcrete/Caliche*) (e.g., Hopley, 1982; Webster and Davies, 2003). This depositional sequence is a firm directional sea-level indicator, although verifying the in situ condition and the time lag between inundation and coral growth is challenging. Sedimentary facies and/or species assemblages (biofacies) within the structure of many reefs have been interpreted as diagnostic of reef initiation, catch-up, and growth at sea level (e.g., Neumann and MacIntyre, 1985; Montaggioni and Faure, 1997); some researchers have described subfacies and biofacies within these larger divisions that may track sea level even more precisely (e.g., Montaggioni et al., 1997; Webster et al., 2009).

Sea level and sedimentary style are plausibly linked; for example, sand aprons prograde leeward of many GBR reef flats, with subtidal sands fining upward but intertidal sands coarsening upward (Davies, 1983). If preserved, these sequences – and their juxtaposition – may comprise a directional sea-level indicator, or possibly a coarse but finite sea-level indicator if reef flat corals are also identified (Davies and Montaggioni, 1985). The vertical distribution of reef taxa along depth-related environmental gradients is similarly credible, with many descriptions

and explanatory models for the zonation of coral reef assemblages available (e.g., Wells, 1954; Done, 1983; Davies and Montaggioni, 1985). However, these distributions are influenced by both physical and biological interactions, which may be very complex and variable between locations and through time, and thus reef assemblages have not been widely used as finite sea-level indicators as the reproducibility and precision with which they record sea level is generally low.

The best-known coral species used as a sea-level indicator is *Acropora palmata* (see *Acropora*) – a shallow-water coral normally restricted to within 5 m of the sea surface. *Acropora palmata* grows in the Caribbean where it forms monospecific communities. Its presence has been used to define when a reef is in shallow water, and to identify keep-up reefs in which vertical accretion tracked sea-level rise (Lighty et al., 1982; Toscano and Macintyre, 2003). Assemblages of corals and coralline algae have been argued as depth definitive (Montaggioni and Faure, 1997; Montaggioni et al., 1997), but as discussed above the precision of these relationships is generally low and the interpretation controversial (Blanchon, 1998). Corals are, however, zonally distributed across environmental gradients including depth and wave energy, and various coral morphotypes are stratified across these zones (Chappell, 1980). The Atlantic-Caribbean massive coral *Montastrea annularis* adopts a platy morphology at depth where light is limited (Woodroffe, 2003), for example, and *Pocillopora damnicornis* colonies are more robust in shallower higher wave-energy habitats (Mass and Genin, 2008). Where the steepness of these gradients can be understood and calibrated reliably to depth, morphotypic variation in corals may be used to reconstruct sea-level histories. This is likely to be most fruitful in the Caribbean where the Holocene sea-level history has promoted the development of keep-up reefs dominated by framework structure. Where detrital sediments dominate the internal structure of reefs, like the GBR (Hopley et al., 2007), reconstructing sea levels by comparing extant taxa and/or morphotypic depth distributions with those recovered in cores is difficult. The use of coral or coral reef material as sea-level indicators in high-energy or storm-prone settings is problematic as material can be transported above growth position and sea level overestimated without careful verification of in situ status.

Algal rims are distinctive reef crest features on many mid-Pacific atolls and some higher-energy Atlantic reefs (e.g., Nunn, 1993), and a coralline algal ridge, particularly of the pink algae *Porolithon*, indicates reef growth near the sea surface (near MLWS, but higher in higher-energy settings (e.g., Woodroffe et al., 2004)) (Figure 2) (see *Algal Rims*; *Algae, Coralline*). Thick algal encrustations are normally restricted to within 4–6 m of the sea surface, but distribution above and below sea level can differ with wave energy. Algae species and morphology systematically vary with depth and wave exposure (Davies and Montaggioni, 1985). Adey (1986), reviewed coralline algae occurrence, and potential use as sea-level indicators,





**Sea-level Indicators, Figure 2** Algal rim at outer edge of reef flat at South Island, Cocos (Keeling) Islands, Indian Ocean.

suggesting that for several species with well-defined ecological niches precision of  $\pm 10$  cm may be realized.

### Microatolls

Microatolls are intertidal corals with dead, relatively flat upper surfaces surrounded by an annular rim of living coral (Figure 3a) (see *Microatoll*). They form when upward coral growth is constrained by prolonged exposure near low water, but polyps on the sides remain alive and continue to grow laterally (Scoffin and Stoddart, 1978; Woodroffe and McLean, 1990). Microatolls are amongst the most precise, geologically persistent, and useful finite sea-level indicators found on coral reefs (Davies and Montaggioni, 1985). Their flat upper surfaces confirm that the coral, and the reefs they overlie, have vertically accreted to the intertidal, and they have been widely used as sea-level indicators because the elevation of their upper surfaces and the sea surface closely correspond.

The exact elevation at which upward coral growth is restricted and a microatoll develops varies between species, and with exposure to wavelet wetting, diurnal and seasonal tidal patterns, and a variety of other factors. However, a high degree of reproducibility of elevation is usually observed between microatolls within the same “field.” On the mesotidal central GBR, the tops of neighboring *Porites* microatolls within a field were within  $\pm 10$  cm (Chappell et al., 1983), and on microtidal mid-ocean reefs microatoll tops in a single habitat varied even less ( $\pm 5$  cm) (Smithers and Woodroffe, 2000). Microatolls on the GBR in habitats freely connected to open water – where the rise and fall of the tide is unimpeded by reef topography – are elevated around MLWS (Scoffin and Stoddart, 1978). At the microtidal Cocos Keeling Islands, most open water microatolls grow above this tidal datum,



**Sea-level Indicators, Figure 3** (a) Living *Porites* microatoll, on reef flat at Poruma, Torres Strait; (b) Fossil *Porites* microatoll >6,000 years old, Iris Point, Great Barrier Reef (GBR), Australia.

with the modal elevation approximately halfway between MLWS and mean low water neaps (MLWN) (Smithers and Woodroffe, 2000). This difference probably reflects the proportionally larger influence of waves on modifying the tidal levels that restrict upward coral growth at Cocos and other mid-ocean microtidal reefs; microatolls at the Cook Islands are also constrained midway between MLWS and MLWN (Goodwin and Harvey, 2008).

Microatolls may grow to several meters in diameter and vary from centimeters to meters in thickness, but most are 1–2 m across and less than 0.5 m high. Both massive and branching corals form microatolls; however, those developed by massive corals are more common and better preserved. The excellent preservation potential of microatolls is demonstrated by the common occurrence of fossil microatolls of mid-late Holocene age on Indo-Pacific reef flats (Figure 3b) (see references below); they are rare in the Atlantic-Caribbean as sea level there has only recently been reached. Modern microatolls often grow in sight of fossil microatolls, and their elevations can be compared directly and surveyed to a tidal datum. Fossil microatolls are well suited for both radiocarbon and uranium-series dating, and thus histories of sea-level change can be established. Chappell et al. (1983) used this approach to determine late Holocene sea-level change on the central GBR, and it has also been applied to establish sea-level histories elsewhere in the Pacific (e.g., Pirazzoli and Montaggioni, 1986; Pirazzoli et al., 1987; Goodwin and Harvey, 2008) and Indian Oceans (e.g., Woodroffe et al., 1990; Kench et al., 2009).

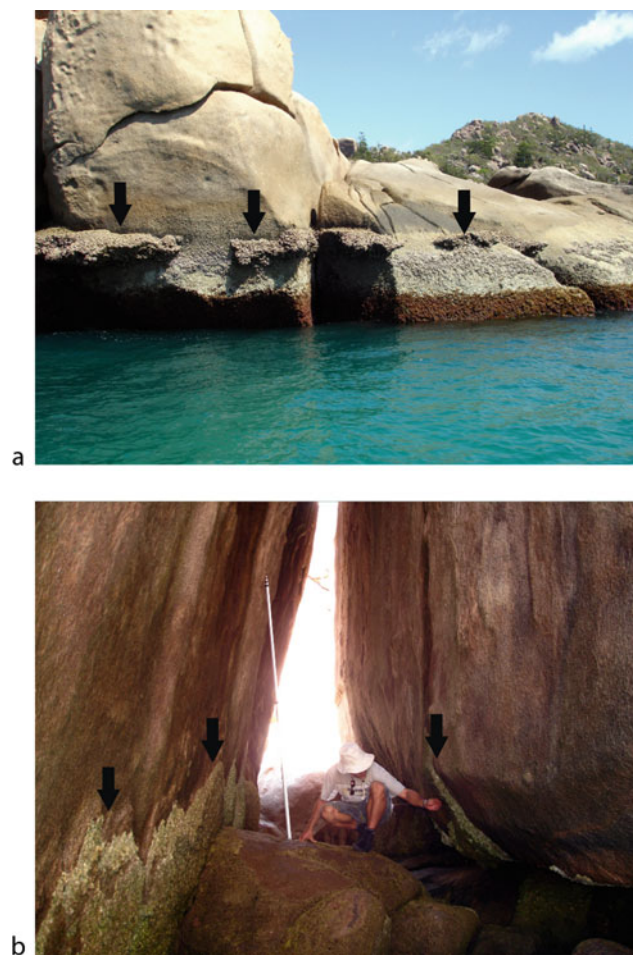
Microatolls can also be used to reconstruct interannual changes in sea level with high precision. Microtopographic undulations over the upper surfaces of well-preserved microatolls track interannual variations in the elevation of the confining water level, within the limits of coral growth (Woodroffe and McLean, 1990; Smithers and Woodroffe, 2001) (see *Microatolls* for detailed description). Annual growth bands are revealed within microatoll skeletons when slices taken through the growth axis are either X-rayed or illuminated with UVB light, and these define a chronology for the upper limit to coral growth for each band (and by inference the height of the confining water level) (see *Sclerochronology*). Back-counting bands (years) from the living annulus at the time of sampling enables sea-level records to be reconstructed that extend back over the coral's lifetime. For a colony a meter in diameter, this would be around 50 years, but may include several centuries for larger specimens several meters across. When microatolls with overlapping life spans are found, their records can be cross-correlated and combined to extend the record. This approach can also be applied to well-preserved and radiometrically dated fossil microatolls of overlapping age (Yu et al., 2009).

Microatolls are excellent sea-level indicators. However, several issues need consideration when they are used. Verification is required that they: (a) are microatolls and not “pseudomorphs” with planar tops caused by erosion (confirmed by examining a colony's internal

structure), (b) are in situ and have been undisturbed by storms or other agencies, (c) grew in an open-water habitat (see Davies and Montagnoni (1985) for diagnostic criteria for open-water microatolls) and are not moated (see *Moating*; *Moats*); and finally (d) when sampling microatolls for dating, sample location should be systematically selected and replicated when inter-colony and site comparisons will be made. *Ad hoc* sampling across large microatolls several meters in diameter (e.g., randomly between perimeter and centre) may introduce age uncertainties exceeding 100 years.

### Oysters and encrusters

Encrusting organisms including oysters and barnacles occupy well-defined vertical zones on intertidal shores (Figure 4a) and have been used as sea-level indicators on tropical reef coasts, including those in the Southern China (Davis et al., 2000), Japan (Pirazzoli et al., 1985), Vietnam (Boyd, 2004), and the GBR (Beaman et al., 1994; Lewis



**Sea-level Indicators, Figure 4** (a) Modern oyster visor, exposed shoreline, Balding Bay, Great Barrier Reef (GBR), Australia; (b) Fossil oyster beds in sea cave at same location, used to infer 1.65 m higher sea level during mid-Holocene.



et al., 2008). Collectively these sessile intertidal organisms are commonly referred to as “fixed biological indicators” (FBIs). They are highly sensitive to long-term changes in water depth, and thus have great potential as sea-level indicators (Laborel, 1986; Pirazzoli, 1991).

The vertical range of FBIs is dependent on the tidal range and exposure to waves. On the central GBR, where the tide range is ~4 m, FBIs are confined with a 1.5 m interval that approximates the neap tide range (Lewis et al., 2008). Sea levels are determined by comparing the relative elevation of the upper and lower boundaries of fossil and extant species at the same locality. The precision of sea levels derived from these deposits may improve to within  $\pm 0.10$ – $0.25$  m if the relative relationships between different encrusters are carefully analyzed (Beaman et al., 1994; Baker and Haworth, 2000).

Davis et al. (2000) describe a mid-Holocene oyster bed at Big Wave Bay in Hong Kong at 1.7 m above a modern equivalent, but neither identifies the species nor reduce the height to a datum. *Ostrea* sp. oysters were used to establish sea-level history on the north coast of Vietnam, where fossil oysters in growth position were identified on near vertical limestone cliffs and in notches eroded into the cliff base. At this site, the fossil evidence is adjacent to modern oysters (Boyd, 2004). Modern *Ostrea* sp. oysters at the Vietnam study site extend from below low tide to around the mid-tide level. On the GBR, the oysters *Saccostrea cucullata* and *Crassostrea amasa* form conspicuous encrustations from MSL up to mean high water neaps (MHWN), although the upper and lower extent of *C. amasa*, and the precise elevation and range of *S. cucullata* encrustations vary widely within this range (Endean et al., 1956). *S. cucullata* forms distinctive visors 0.3–0.6 m thick between MHWN and MSL (Beaman et al., 1994), with the exact elevation varying with exposure. Lewis et al. (2008) suggested that *S. cucullata* could be restricted to vertical zone just 0.2–0.4 m wide (where tidal range is ~4 m), and argued these oysters allow robust reconstructions of paleo-sea level if the internal structure of a bed can be established and oyster age and elevations are accurately determined relative to modern oysters.

Barnacles and tube worm agglomerations have also been used as sea-level indicators on coral reefs (Pirazzoli et al., 1985; Baker et al., 2001; Lewis et al., 2008), although the later are more abundant on temperate coasts. Endean et al. (1956) detailed the vertical distributions of a range of intertidal organisms on Queensland's coastal islands, and considered that the barnacles *Octomeris brunnea* and *Tetraclitella* sp., which form crusts with high preservation potential, were particularly promising sea-level indicators. Pirazzoli et al. (1985) also concluded that *Octomeris* barnacles had great potential as very precise indicators of higher sea level stands in the Ryukyu Islands, but noted they are easily eroded after death if they remain in the intertidal. On the GBR, barnacles also tend to define higher sea levels. Lewis et al. (2008) suggested a barnacle 1.35 m above present sea level dated at 7,400 years BP was evidence for an earlier highstand on the central

GBR. A calibrated radiocarbon age of 5,310 years also exists for fossil barnacles located in a cave at Magnetic Island, offshore from Townsville (Beaman et al., 1994), but for the reasons discussed below, their sea-level significance remains ambiguous.

Unless buried or protected by rockfalls, encrustations are poorly preserved on open coasts as the rocks to which they attach are weathered and eroded (Scoffin, 1977). Fossil FBIs thus tend to be located at protected sites where the indicative meaning can be difficult to assess. For example, a fossil encrustation of *S. cucullata* in a protected cave at Balding Bay on Magnetic Island is ~1.65 m above the modern oyster bed. This fossil crust is presented as evidence of mid-Holocene sea levels 1.65 m above present persisting until around 4,000 years ago (Beaman et al., 1994), although it is arguable whether the fossil oyster's protected habitat is comparable to the modern oyster's exposed position (Figure 4b).

For most FBIs, interplay between growth and erosion means that long and continuous sea-level records are rare. Most encrustations are exposed to wave erosion, and if the rate of sea-level change is slow – or stable – the encrustation remains vulnerable to erosion. Rapid sea level falls that elevate the FBIs above the zone of wave attack offer the best prospects for FBI preservation. In the case of slowly rising sea levels, the entire encrustation assemblage may shift upwards, with a systematic vertical translation of species. Where change is fast, the encruster's response may not be sufficient to track it. Encrustations appear best to be able to document stillstands or slow sea-level changes, at which visors that extend tens of centimeters out from the rock surface may form. Over time this geometry increases vulnerability to breakage during storms, and intrinsically constrains the length and continuity of records preserved by these structures.

### Beachrock and cemented deposits

Beachrock is the lithified deposit formed when calcium carbonate cements consolidate beach sediments (see *Beach Rock*). Lithification occurs on relatively stable beaches beneath a cover of loose sediments that are later eroded to expose the beachrock outcrop (Figure 5). Beachrock can form in beaches composed of fine sands to boulders of terrigenous or biogenic provenance. Sedimentary structures such as bedding planes are preserved in many beachrocks. Some beachrocks are weakly cemented, with only the outer crust firmly indurated, but highly indurated massive beachrocks more than a meter thick also occur. The processes and conditions for beachrock formation and cementation have been well studied and debated (see Russell and MacIntyre, 1965; Stoddart and Cann, 1965; Hopley, 1986a); these details are not repeated here. Beaches on mainland shores, cays (see *Coral Cay Classification and Evolution*), and high islands may all host beachrock.

Beachrock durability and the consistency with which it forms within the intertidal have enticed researchers to use



it as a sea-level indicator. The exact upper limit of formation is, however, often poorly constrained, particularly where the tidal range and/or wave energy are high (Hopley, 1986a). The vertical dimensions of a beachrock outcrop vary with tidal range, with more compact beachrocks developing where tides are smaller. The upper limit is commonly around MHWS, but the precise upper limit to cementation is difficult to define as the degree of cementation often grades up the beach. This may partly reflect the rapidity with which cementation can occur (e.g., beachrocks on Magnetic Island developed in 6 months (Hopley, 1986a)). As cementation is so swift, it is possible that incipient beachrocks may form at infrequently achieved tidal levels if beaches are sufficiently stable.

Exposure to waves contributes further variability, with beachrocks on shores exposed to higher wave energy usually developing at higher elevations and being of greater vertical and horizontal extent. Kelletat (2006) argued that many beachrocks may be supratidal, but this is a minority view (Knight, 1997). On the northern GBR where the upper limits of modern beachrocks are between 1.6 and 2.9 m above tidal datum, MHWS is around 2.3 m (Davies and Montaggioni, 1985). Hopley (1986a) assessed the problems of reliably assigning an indicative meaning to beachrock elevation and concluded that the upper limit of beachrock formation should conservatively be considered to be as high as the highest astronomical tide (HAT). Uncertainties regarding whether the top of a paleo-beachrock reliably reflects a tidal level, swash effects, or is possibly an erosion surface demand that they be cautiously used as indicators of past sea level. The base of beachrock outcrops commonly lies near MLWS but this offers little utility for sea-level investigations as cementation may have occurred as the sea rose above this level at an earlier stage of lithification.

The efficacy of beachrocks as reliable sea-level indicators is further diminished by difficulties encountered in

establishing the age. Constituent bioclasts may be radiometrically dated to derive a maximum age, but this assumes that the bioclasts were incorporated soon after the contributing organism died (see *Radiocarbon ( $^{14}\text{C}$ ): Dating and Corals*). Calcium carbonate cement must be dated to determine a minimum age for the deposit, but this is technically difficult. Enough uncontaminated cement is difficult to harvest, and the possibility of multigenerational cementation and rejuvenation of the apparent age presents problems. Where beachrocks contain some quartz luminescence, dating – which establishes a depositional age – has been applied and produced promising preliminary results; paired luminescence and radiocarbon ages reveal the latter are systematically older by several hundred years, which may be attributed to the death to deposition lag (Thomas, 2009). Finally, although many beachrocks document former shoreline positions and have remained in situ, large beachrock slabs are dislodged by storms, and may be recemented intact but out of their original position. Only in situ beachrock should be used as a sea-level indicator.

Conglomerate platforms can be similar in appearance and elevation to coarse beachrock (see *Conglomerates*), but typically occur as subhorizontal platforms of poorly sorted cemented storm detritus (Montaggioni and Pirazzoli, 1984). Conglomerates around 1 m thick form platforms over windward reef flats on many Pacific reefs, and commonly form the foundations for reef islands (Figure 6). They are generally interpreted as storm deposits that accumulated near to sea level, an interpretation supported by the occurrence of in situ fossil microatolls over and sometimes within these deposits (Woodroffe et al., 1990). They are generally emergent features now perched above their contemporary equivalents – storm deposited gravel and boulder sheets (Pirazzoli and Montaggioni, 1986) – following sea level falls during the last few thousand years (Woodroffe, 2003).

Close petrographic examination of cements that bind conglomerates in French Polynesia identified two distinct sequences of marine cementation, the boundary between which marks the position of the marine water table. This boundary is generally close to mean low tide but locally varies with deposit permeability and reef flat drainage (Pirazzoli and Montaggioni, 1986). Below the boundary, cementation has occurred in both a marine phreatic and then a vadose environment, whereas above the boundary only vadose zone cements are present. Phreatic cementation overprinted by vadose cements suggests a sea level fall. Montaggioni and Pirazzoli (1984) conclude that conglomerates cannot be used to define the exact magnitude of a sea level fall, but are very useful indicators of sea-level change tendency in areas of low tidal range. The problems of dating beachrocks are all confronted with conglomerates, although as indicated above, in situ fossil microatolls buried beneath or growing over these deposits allow the ages of some conglomerates to be bracketed.

Other cemented outcrops including cay sandstones, dune eolianites, coffee rock, and silcrete that superficially



**Sea-level Indicators, Figure 5** Beachrock exposure at Heron Island, southern Great Barrier Reef (GBR).

resemble beachrock but have no consistent relationship to sea level also occur on reef coasts. Separate entries on phosphatic cay sandstone and eolianite should be consulted for details of description and formation (see *Phosphatic Cay Sandstone*; *Eolianite*). Both deposits are formed by supratidal lithification involving phosphatic or carbonate cements, and are hence useful directional sea-level indicators. For example, phosphatic cay sandstone forms when phosphatic cements derived from bird guano percolate sediments to the water table (Hopley, 1982), which on low islands and backshores can be close to sea level. Where relative sea levels change, this relationship may be altered – phosphate rock low in the tidal may indicate that sea levels have risen after deposit formation, but may also reflect changes in island shape and hydrology (see *Coral Cays – Geohydrology*).

### Mangrove deposits

Mangroves occur throughout the tropics in sheltered settings on shelf and mid-ocean coral reefs (see *Mangroves*). With only rare exceptions, mangroves grow in the

intertidal, mostly between MHWS and MLWS. Individual mangrove species have narrower vertical ranges that may yield even higher resolution sea-level signals if in situ stumps or roots are identified, but in complex habitats with increased diversity other factors may complicate these interpretations. For example, the vertical range of mangroves of the same species located less than 20 km apart varied by 0.5 m in North Queensland due to local differences in tidal behavior (Bunt et al., 1985). Such variability is problematic for precise sea-level reconstruction, especially where coastal and tidal configurations have changed through the Holocene. Larcombe et al. (1995) suggest an error of  $\pm 1.5$  m be applied on the GBR when measurements are not available, but on microtidal mid-ocean reefs this error may be reduced.

Mangrove deposits are either peats or muds. Mangrove peats are highly organic deposits dominated by mangrove-derived macrofossils (Figure 7). They are typical of microtidal environments with low terrigenous influx



**Sea-level Indicators, Figure 6** (a) Conglomerate platform with reef island above at Takuu, Papua New Guinea. (b) Exposure through conglomerate platform at Maiana, Kiribati.



**Sea-level Indicators, Figure 7** (a) Mangrove peat with in situ stumps preserved at shoreline of Madhiravadhoo, Maldives. (b) Close-up of peat in (a) showing gastropods associated with mangrove habitat.



(Woodroffe, 1988). Kelletat (1988, p. 227) stated that “the closest approximations to the mean sea level are provided by the base of the mangrove peat because these plants very precisely occupy the upper half of the tide range,” but he provided no data to support this claim. Mangrove peats have been used to infer late-Holocene sea-level changes on Caribbean and Pacific coral reefs, but the interpretations derived from them are controversial (Bloom, 1970; Woodroffe, 1988; Toscano and Macintyre, 2003; Blanchon, 2005). On the GBR, mangrove peats are restricted to offshore islands, or exposed shorelines where finer material is winnowed away. Mangrove *muds* are dominated by fine terrigenous silts and clays but contain mangrove pollen and sometimes remnants of mangroves and mangrove community associates such as oysters and other molluscan fragments (Grindrod and Rhodes, 1984). They are usually gray or grayish olive and buttery in texture. Mangrove muds mostly occur on reef coasts with large terrestrial catchments, where they overly beach and shallow sub-tidal sands and are interpreted as transgressive deposits (Grindrod and Rhodes, 1984).

Local variations in the indicative meaning of mangrove deposits, and of deposit taphonomy must be recognized when using them as sea-level indicators. Mangrove elevation may vary spatially as tidal curves differ geographically or through time, and can also be influenced by factors other than sea level, such as freshwater influx. Especially on exposed coasts, mangrove deposits are vulnerable to reworking during storms, and many mangrove deposits on shelf reefs were reworked during the postglacial transgression. Compaction and/or organic degradation can also lower a deposit, resulting in sea levels being underestimated. Postdepositional modifications are minimized where peats are thin and overlie less compactable strata such as bedrock or beach sands (Toscano and Macintyre, 2003), although Woodroffe (1988) suggested that greater root penetration from younger mangroves may increase compaction in thin peat deposits. Compaction of 10–20% is estimated for Holocene mangrove sequences overlying Pleistocene clays on the central GBR (Larcombe et al., 1995).

Well-preserved mangrove wood can be radiocarbon dated, and where it is in situ, its position on the plant can be identified (e.g., a buttress root), and it is proximal to modern counterparts, both relative elevation and age can be determined. Accurately and precisely dating mangrove muds is more difficult as the bulk samples necessary to harvest sufficient organics may integrate carbon with a wide range of true ages. Accelerator mass spectrometric (AMS) dating requires much smaller samples and can reduce the potential size of these errors, but cannot overcome issues of deposit reworking. The preservation of mangrove deposits (and materials) appears to have been improved during periods of rapid transgression, when increased depth rapidly isolated them from erosive shore processes and in some cases resulted in their burial (Hull, 2005). Woodroffe (1988) concluded that mangroves are good indicators of rapid transgression over millennia in

the stratigraphic record, but were poor sea-level indicators during periods of slow sea level rise, stillstand, or emergence due to issues of reworking and poor preservation.

### Marine notches

A marine notch is an indentation that may be centimeters to meters deep and of similar dimensions from base to top formed by erosion on coastal cliffs. They are prominent relative sea-level markers where uplift has exposed older reef limestones at the coast (Figure 8), and modern and fossil notches occur on the same cliff. Marine notches are formed during periods of relatively stable sea level, and hence multiple notches are required to establish a history of sea-level change. They are typically formed by a combination of corrosion and bioerosion (Dickinson, 2001), and achieve a morphology that reflects lithology, tidal traits, and wave exposure. The continuity of notch morphology through sites sheltered from vigorous wave action suggests that biological processes and solution are important in notch formation (Woodroffe, 2003). On coral reef coasts, marine notches are often asymmetric, with a gently inclined floor and prominent visors forming the roof (see *Notch and Visor*). Pirazzoli (1986, 1996) reviewed the various classifications and types of marine notches, and has linked key features of notch profile to tidal datums. He suggested that the base of modern marine notches was most often (in sheltered sites) close to the low tide level, with the retreat point coinciding with MSL, but others working in the Pacific contend that the retreat point is more often near the high tide level (Dickinson, 2001).

Different interpretations of the indicative meaning of notch features introduces uncertainty when they are to be



**Sea-level Indicators, Figure 8** Double notch on uplifted reef, Buka Channel, Bouganville, Papua New Guinea.



Sea-level Indicators, Table 1 Sea-level indicators on coral reefs – summary

| Indicator          |                            | Finite/<br>directional   | Elevation precision<br>(indicative<br>meaning)                                 | Preservation | Dating | Comments                                                                                                                                                                                                                                                                                                                                                                                                                                                                                                      |
|--------------------|----------------------------|--------------------------|--------------------------------------------------------------------------------|--------------|--------|---------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Coral reefs        | Without reef flat features | Directional              | Poor (50 m to MLWS)                                                            | Good         | Good   | Good directional indicator, but indicative meaning ambiguous.                                                                                                                                                                                                                                                                                                                                                                                                                                                 |
|                    | With reef flat features    | Finite                   | Good (–5 m to MLWS)                                                            | Good         | Good   | Depends on setting and features available.                                                                                                                                                                                                                                                                                                                                                                                                                                                                    |
| Corals             | <i>Acropora palmata</i>    | Directional and finite   | Good (–5 m to MLWS)                                                            | Good         | High   | Caribbean only. In situ colonies indicates SL within 5 m. Rapid growth rate so thick frameworks also good directional indicator useful for transgressive sea levels – can be used with other features (coralline algae, other biofacies) to reconstruct transgressive history.                                                                                                                                                                                                                                |
|                    | Species assemblages        | Directional and finite   | Indicative meaning varies with assemblage<br>Precision variable – fair to good | Good         | High   | Biofacies with different compositions used to reconstruct depth changes related to sea-level change and framework growth. For example, at Mauritius, Montaggioni and Faure (1997) identified:<br>a <i>Pachyseris/Oulophylia</i> biofacies >20 m depth, an <i>Acropora</i> “tabulate” and Faviid community (20–6 m depth), a robust branching <i>Acropora</i> community (<6 m depth), and a <i>Pavona</i> community (<10 m). Different species and morphologies offer potential for improved depth resolution. |
|                    | Microatolls                | Finite                   | High. GBR open water (MLWS); moated (to MLWN). Mid-ocean (~MLW)                | High         | High   | Elevations vary with species. Massive <i>Porites</i> most commonly used. Excellent precision, reproducibility and preservation potential. Widely used in Indo-Pacific. Less common in Atlantic-Caribbean due to sea-level history.                                                                                                                                                                                                                                                                            |
| Sedimentary facies |                            | Directional, some finite | Indicative meaning varies with facies<br>Precision variable – poor to good     | Poor to fair | Poor   | Intertidal facies have greatest potential as both finite and directional indicators, but low preservation potential and as often detrital, low age resolution. Some may, however, become cemented and be better preserved.                                                                                                                                                                                                                                                                                    |
| Coralline algae    |                            | Finite                   | Most common in depths shallower than 2 m MLWS                                  | Good         | Good   | Very useful if preserved. Different species and morphologies offer potential for improved depth resolution.                                                                                                                                                                                                                                                                                                                                                                                                   |
| Molluscs           | Oysters                    | Finite                   | Intertidal                                                                     | Fair         | Good   | Different species have well-defined vertical ranges. Tend to be best preserved in protected settings difficult to compare directly with open water modern counterparts. Dating deposit age is difficult.                                                                                                                                                                                                                                                                                                      |
|                    | Barnacles                  | Finite                   | Intertidal                                                                     | Fair         | Good   | As for oysters.                                                                                                                                                                                                                                                                                                                                                                                                                                                                                               |

Sea-level Indicators, Table 1 (Continued)

| Indicator         | Finite/<br>directional    | Elevation precision<br>(indicative<br>meaning)                                      | Preservation                         | Dating          | Comments                                                                                                                                                                                                                                                                                                 |
|-------------------|---------------------------|-------------------------------------------------------------------------------------|--------------------------------------|-----------------|----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|
| Beachrock         | Finite                    | To HAT, but may<br>be lower                                                         | Fair                                 | Low             | Intertidal formation though upper<br>limit can be difficult to define.<br>Dating very difficult. Can be<br>confused with supratidal<br>cemented deposits, although<br>cement type should resolve<br>identity.                                                                                            |
| Conglomerate      | Finite                    | MSL +1 m. Vadose/<br>phreatic cement<br>boundary<br>~MLW                            | Good                                 | Fair            | Interpreted as forming near to<br>MLW on storm-exposed flats.<br>Cemented initially in marine<br>phreatic environment, and then<br>partially in vadose zone as sea<br>level falls leave deposit<br>emergent. Cement boundaries<br>can improve indicative<br>meaning. Dating deposit age is<br>difficult. |
| Mangroves         | Finite and<br>directional | Intertidal, mostly<br>between MHWS<br>and MLWS                                      | Fair to poor                         | Poor to<br>good | Transgressive deposits best<br>preserved as isolated from<br>destructive processes that<br>degrade still stand deposits.<br>Deposits vulnerable to<br>compaction and erosion.<br>Integration of roots and<br>reworked older carbon can<br>make dating difficult.                                         |
| Microfossils      | Finite and<br>directional | Subtidal and<br>intertidal – varies<br>with species and<br>assemblages              | Can be good,<br>setting<br>dependent | Fair            | Reportedly can achieve<br>elevational precisions of $\pm 7$ cm<br>with statistical treatment of<br>data, but yields outcomes at<br>odds with other indicators.<br>Dating difficult due to small<br>size of materials and possibility<br>of reworking. New technique<br>on reefs with potential.          |
| Marine<br>notches | Finite                    | Intertidal. Retreat<br>point variably<br>argued to mark<br>MSL or high tide<br>mark | High                                 | Fair            | Varying interpretations of<br>morphology and relationship<br>with tidal datums. Dating relies<br>on encrusters, which can be<br>problematic.                                                                                                                                                             |

used as sea-level indicators but this is not a problem where sea-level changes are inferred from the differential elevations of modern and fossil features on the same cliff. The retreat points on modern and fossil notches tend to be well defined allowing relative elevations to be directly and relatively precisely measured. However, dating notches is more difficult, and usually involves dating encrusting shells (Nunn, et al., 2002; Boyd, 2004) and/or correlation with other dated features (Koba et al., 1982; Dickinson, 2001). Stalactites and flowstones may have formed on ancient notches since emergence, and may be dated to derive a minimum age of notch formation. Notches also occur on currently submerged reefs, and have similarly been used to establish former sea levels (Grigg et al., 2002).

### Microfossils

Microfossils such as pollen and foraminiferan tests have been used as sea-level indicators on the GBR, but are yet to be widely applied on other reefs. The approach exploits the tendency of many foraminiferans to occupy narrowly defined environmental niches that often stratify according to tidal levels (e.g., Gehrels, 1994). Where foraminiferans are well preserved in situ, they are useful indicators of sea level. Assemblages associated with broader tidal or environmental zones have been identified within the GBR (Haslett, 2001), but elevational precision is often poor.

The foraminiferan “transfer function” approach has been applied to develop precise sea-level records from foraminiferan data in temperate salt marshes and has recently been used on the GBR. A precision of  $\pm 0.07$  m

was reported for mesotidal mangrove coasts near Townsville (Horton et al., 2003) suggesting this technique has great promise for reconstructing sea-level histories on other sedimentary coastlines in reef settings where high-precision sea-level indicators such as microatolls and encrusting oysters are poorly represented. However, some difficulties with this methodology are evident where it hindcasts sea levels significantly above those documented by other indicators (Woodroffe, 2009). Foraminiferans are small and light; age is usually determined by AMS dating a bulk sample of foraminiferan tests picked from sediment under a microscope.

### Other indicators

A range of other geomorphic or sedimentological features with more limited application have also been associated with sea level on reefs. These include intertidal facies (Harvey et al., 2001); freshwater swamp, fluvial and other terrestrial facies or materials (Hopley, 1970); shore platforms, reef islands, boulder tracts and ramparts (Scoffin, 1977; Hopley, 1982; Davies and Montaggioni, 1985), and bioerosion and cementation signatures (Scoffin, 1977; Gischler and Lomando, 1997).

### Summary

The key attributes of the major sea-level indicators described above are summarized in Table 1.

Coral reefs are clearly rich repositories of sea-level information, with a great variety of sea-level indicators found in these environments. The quality of the sea-level data yielded by these indicators is variable in precision (elevational and age), and in the resolution with which sea level is actually and preserved. The most precise sea-level indicators record stillstand or small magnitude and/or slow sea-level changes, with only mangrove deposits and *Acropora palmata* frameworks documenting periods of rapid transgression. It is probable that improved technologies for detecting sea-level features and measuring their elevation – such as RTK GPS and swathe mapping – and also for harvesting material and establishing ages will improve the precision of data yielded from sea-level indicators from reefs into the future.

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## Cross-references

[Acropora](#)  
[Algae, Coralline](#)  
[Algal Rims](#)  
[AUVs \(ROVs\)](#)  
[Barbados](#)  
[Bassett Edges](#)  
[Beach Rock](#)  
[Calcrete/Caliche](#)  
[Conglomerates](#)  
[Coral Cay Classification and Evolution](#)  
[Corals: Environmental Controls on Growth](#)  
[Diagenesis](#)  
[Earthquakes and Emergence or Submergence of Coral Reefs](#)  
[Ecomorphology](#)  
[Emerged Reefs](#)  
[Eolianite](#)  
[Florida Keys](#)  
[Fringing Reefs](#)  
[Geomorphic Zonation](#)  
[Glacio-Hydro Isostasy](#)  
[Holocene High Energy Window](#)  
[Huon Peninsula, P.N.G.](#)  
[Mangroves](#)  
[Meltwater Pulses](#)  
[Microatoll](#)  
[Moats](#)  
[Moating](#)  
[Notch and Visor](#)  
[Phosphatic Cay Sandstone](#)  
[Postglacial Transgression](#)  
[Radiocarbon \(<sup>14</sup>C\): Dating and Corals](#)  
[Reef Classification, Response to Sea Level Rise](#)  
[Sclerochronology](#)  
[Submerged Reefs](#)  
[Swathe Mapping](#)  
[Uranium Series Dating](#)

## SEDIMENT DURABILITY

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### Definition

The ability of sediment constituents to resist destruction by physical forces.

### Introduction

The composition of calcareous reef sediment is a function of skeletal production by calcifying organisms; the destruction of skeletal remains by physical, biological, and chemical processes and sorting/mixing processes. The ability of detrital reef sediment to resist destruction by physical processes is a direct outcome of the durability of the sediment constituents. Highly durable constituents are less susceptible to physical destruction. Consequently, increasingly durable constituents are more likely to be present within sediment, which has endured significant transport and mixing. The degree to which the durability of constituent material is expressed in the composition of sediment is the function of the rate of sediment generation and the exposure to destructive processes. Highly durable, yet less productive, constituents can provide significant material to sedimentary systems, likewise highly productive, yet less durable, constituents can ultimately contribute little to a deposit, which will endure significant transport/mixing.

The physical destruction of reef-derived skeletal remains is driven by the entrainment and transport of material by hydrodynamic processes. Physical destruction and mechanical breakdown are terms used to group the processes of fragmentation and abrasion. Fragmentation is the physical fracturing of remains into discrete units (Lyman, 1994). In contrast, abrasion involves remains being physically ground down by collisions with other material resulting in a loss of mass and smoothing of the surface (Meldahl, 2001). The physical breakdown of reef framework and the skeletal remains of occupying organisms is widely considered to occur during high-energy events, that is, storm conditions (Scoffin, 1992; Grigg, 1995).

### Determining sediment durability

The durability of sediment and skeletal remains has been widely studied in both fields of sedimentology and paleontology. A range of techniques have been developed and applied to experimentally determine the physical durability of clasts. Primarily, these involve apparatus designed to replicate the destruction of material during transport. These studies can be broadly classified as sedimentological or paleontological studies, depending on the material used and the focus of the study.

Sedimentological studies have commonly focused on the physical abrasion of sediment as measured by change in clast weight. Change in clast weight has been used widely within fluvial systems to explain downstream fining of sediment in rivers, or along sediment transport pathways in coastal settings (see Lewin and Brewer, 2002 for methodological review). In contrast, paleontological studies tend to focus on the transformation of skeletal remains through physical, biological, and chemical processes, through the incorporation within the fossil record (Chave, 1960; Greenstein, 1991; Kotler et al., 1992; Beavington-Penney, 2004).

Nearly, all coral reef sediment comprises the skeletal remains of the reef framework builders and occupying organisms. This unique situation forces the examination of reef sediment to be an exercise in both sedimentology and paleontology. Reef sediments offer numerous challenges to the established methodologies developed with river-bed materials. First, in some of the earliest studies of this kind, Chave (1960) found that the durability of reef material varies more widely than the other types of sedimentary grains. In addition, reef sediments are composed of the skeletal remains of numerous organisms; each potentially displaying different levels of susceptibility to physical destruction, some seemingly delicate while others robust. The different degrees of durability and post-mortem life histories of reef sediment constituents complicate interpretations when compared to the relatively uniform sediment encountered in other coastal settings.

Chave (1960) conducted some of the earliest experiments assessing the durability of various constituents of carbonate sediment. Chave (1960) used a tumbling barrel to examine the abrasion of various reef species, including filamentous calcareous algae, Bryozoa, and various pelecypods, gastropods, corals, and echinoids. He found that the abrasion rates of experimental material varied considerably from total disintegration of Bryozoan clasts within an hour, through to *Nerita* (an intertidal snail), which after 183 h were worn but still recognizable to species level.

In a further study, Moberly (1968) isolated the most common individual components of sand from Hawaiian beaches and abraded them within tumbling barrels. These sediments contained a mix of volcanic material along with sediments of calcareous origin. The individual calcareous components analyzed were coral, *Halimeda*, molluscs, echinoids, foraminifera, and red algae. Moberly (1968) found that molluscs, foraminifera, echinoids, and red algae all display similar size related abrasion relationships. Larger clasts of these four components all produced more sediment after 50 h in the tumbling barrel than smaller clasts. Coral and *Halimeda* samples showed increased abrasion rates in smaller clast sizes. Moberly (1968) suggested that this is a function of the fibrous and spicular structure of the aragonitic corals and *Halimeda*. This is in contrast to Chave (1960), who found little correlation between mineralogy and durability. During tumbling barrel experiments, Hoskin et al. (1983) noted that dead coral yield almost twice as much sediment as living coral.



This was attributed to the abrasion of encrusting organisms and a skeletal structure weakened by bioerosion, suggesting a strong interplay between biological and physical destruction of reef sediment constituents.

Other experimental procedures have been developed and utilized to experimentally study the durability of skeletal remains while under transportation. While different from tumbling barrels, the techniques share a common theme in that a clast is exposed to an abrasive agent in an agitated state to simulate transport. Kotler et al. (1992) found through a series of abrasion experiments using orbital shakers that foraminiferal tests collected from modern reef assemblages at Discovery Bay, Jamaica were robust. However, differences in durability between species were discernible, with some more susceptible to abrasion than others, with some species that were completely destroyed during experimental runs.

### Implications of durability on sedimentary systems

Experimental investigations have found large variations in the relative durability of sediment constituents from various reef settings. While there is a lack of experimental consistency between approaches used to determine durability, there are broadly observed trends as to the ranking of constituent durability. Typically, coral and gastropods are the most durable, followed by foraminifera tests, echinoid spines, and calcareous algae. Physical durability has only been assessed for a limited range of sediment constituents and utility of results is hampered by inability to establish absolute measures of durability. However, there are several implications and uses of establishing the durability of key sediment constituents.

A detailed understanding the postmortem transportation history of sediment constituents can further aid in the selection of material for radiocarbon dating. Woodroffe et al. (2007) found AMS radiocarbon dates of coral grains to be a poor indicator of depositional age within a reef island deposit. This, Woodroffe et al. (2007) argue, is a function of the long period of time that the coral may be retained within the active sedimentary system prior to deposition. Tumbling barrel experiments tend to concur with this observation of higher coral durability, prompting caution when selecting material for radiocarbon dating. Having established that remains of calcareous algae *Halimeda* are rapidly destroyed postmortem, it can be assumed that the lag between time of death and time of deposition is brief, making *Halimeda* an ideal candidate for targeted AMS radiocarbon dating. Understanding of constituent durability is particularly useful in situations where understanding the lag between time of death and time of deposition underpins interpretations.

Similarly, inferences into the deposition of landforms can be strengthened through a thorough understanding of constituent durability. Material comprising carbonate landforms is often used to infer the transport and depositional history of such sediment (McLean and Stoddart, 1978; Yamano et al., 2000; Kench et al., 2005; Woodroffe

et al., 2007). The ability to infer the degree of transport endured by such a deposit can greatly improve such interpretations. For example, it could be argued that a landform comprised of less durable material has either been deposited rapidly or developed under low-energy settings. Reef islands that have been found to be comprised of a high percentage of *Halimeda* indicate a short lag time between sediment generation and island initiation. Kench et al. (2005) documented largely unmodified *Halimeda* facies within Maldivian Islands which they argue are concentrated within the “velu” or shallow lagoon facies. The inability of *Halimeda* to endure significant postmortem transport likely limits its utility in land building to low-energy settings.

### Conclusion

Within reef systems, biological and physical processes play key roles in the breakdown of sediment constituents and drive the formation of sedimentary deposits. The physical destruction of reef material is a significant feature of the sedimentary systems of coral reefs, the importance of which has largely been considered secondary to biological destruction. The susceptibility of sediment constituents to physical breakdown is a function of the durability of skeletal remains and the ability of environmental processes to initiate physical destruction. An understanding of skeletal durability provides unique insights into the postmortem history of constituents comprising a deposit, yielding increased powers to interpret attributes of a deposit.

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## Cross-references

Bioerosion  
Sediment Dynamics  
Sediments, Properties  
Taphonomy

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## SEDIMENT DYNAMICS

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### Definition

*Sediment dynamics.* The process of entrainment, transport, and deposition of detrital sediment within coral reef systems that controls the sediment budget status of a reef platform and development and change of sedimentary landforms within reef systems.

### Introduction

Coral reefs and reef sedimentary landforms are unique in that they are composed predominantly of calcium carbonate ( $\text{CaCO}_3$ ) that results almost entirely from ecological processes. The primary sources of reef carbonate are the skeletons of corals and other organisms or plants that induce  $\text{CaCO}_3$  deposition. Furthermore, their provenance is intrabasinal, with sediment production and deposition occurring either on, or in close proximity to, a reef platform. In addition to ecological processes, chemical precipitation can be locally important in the production of carbonate material (e.g., ooids), while terrestrial inputs can also impact locally on the sediment systems of fringing and barrier reefs.

Production of calcium carbonate by primary frame builders (corals and encrusting coralline algae) is an important component in reef development (Hubbard et al., 1990). Furthermore, carbonate production by primary frame builders and secondary benthic organisms interacts with a range of physical, chemical, and biological processes to “cycle” calcium carbonate within a reef system. Some of these processes aid in reef development; others control the generation of detrital sediment on reef

platforms, which is subsequently reincorporated and cemented into reef framework (Hubbard et al., 1990; Perry et al., 2008), stored on reef surfaces, transported off-reef (Hine et al., 1981; Hughes, 1999), transferred to infill lagoons (Macintyre et al., 1987; Kench, 1998a; Purdy and Gischler, 2005), or build sedimentary landforms such as coastal plains and reef islands (Maragos et al., 1973; Hopley, 1982; Calhoun and Fletcher, 1996; Woodroffe et al., 1999; Yamano et al., 2000, 2002).

As reef platforms constitute the net balance of calcium carbonate deposition in skeletons by primary producers and the redeposition of detrital materials in the reef framework the entire reef framework is considered a sedimentary unit. Typically sediment budget studies have attempted to quantify the net accumulation of carbonate material retained within reef systems (Hubbard et al., 1990; Perry et al., 2008) to establish the pattern of reef platform development at geological timescales. However, such studies have typically treated the generation of detrital material, which is not reincorporated into the reef framework, as losses to the reef system despite its importance in development of sedimentary landforms on or adjacent to reefs.

This entry adopts a view of sediment dynamics that is focused on the production, dispersal, and deposition of detrital carbonate at a range of timescales. The entry presents an overview of the processes that generate detrital sediment in coral reef systems, as these are the building blocks for sedimentary landform development. The mechanics and processes that activate sediment transport are examined, and difficulties in the use of standard sedimentological tools to infer sediment dynamics are discussed. Field studies that attempt to quantify sediment dispersal patterns and rates of transport are identified and discussed in light of the process controls on transport and their control on the development of sediment deposits. Insights into sediment dynamics are also examined based on observations of volumetric changes in sediment stores on reef systems from short to long timescales.

### Sediment generation

Sediment dynamics in coral systems are controlled by a number of processes that include hydrodynamic and biological processes that entrain, transport, and deposit sediments within reef systems. An overriding control is the rate of sediment supply to reef systems.

The supply of sediment in reef systems is principally governed by the production of calcium carbonate and its conversion to detrital material via a suite of physical, biological, and chemical processes.

### Calcium carbonate production

The production of calcium carbonate on reef platforms is modulated by the composition, distribution, and abundance of calcifying organisms on reefs. Producers form two broad groups. Primary producers are those organisms such as scleractinian corals and coralline algae whose skeletons

directly contribute to the framework of a reef platform. Secondary producers include a wide range of benthic organisms (foraminifera, molluscs, calcareous algae, echinoids, crustaceans) that dwell on the reef framework.

Production rates of a range of primary and secondary producers have been studied at the organism level (see Stearn et al., 1977; Hallock, 1981; Vecsei, 2001; Hart and Kench, 2007 for syntheses). Calcification rates for individual organisms range from 1.39 to 17.0 kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ a}^{-1}$  for corals (Hughes, 1987; Eakin, 1992), 0.20–2.3 kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ a}^{-1}$  for coralline algae (Stearn et al., 1977), 0.05–2.2 kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ a}^{-1}$  for the calcareous algae *Halimeda* (Multer, 1988; Drew, 1983), 0.04–0.7 kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ a}^{-1}$  for foraminifera (Sakai and Nishihiro, 1981; Tudhope and Scoffin, 1984), and 0.002–0.55 kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ a}^{-1}$  for molluscs (Richard, 1981; Harney and Fletcher, 2003). A number of studies have also attempted to generate aggregated reef platform production estimates based on hydrochemical techniques (e.g., Smith and Kinsey, 1976; Smith and Harrison, 1977), census-based approaches using data on organism abundance and growth (Chave et al., 1972; Harney and Fletcher, 2003; Vecsei, 2004; Hart and Kench, 2007), geological estimates based on net accumulation of reefs (e.g., Ryan et al., 2001), and modeling techniques (Kleypas, 1997). Typical values from this aggregated approach range from 0.8 kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ a}^{-1}$  for lagoonal environments, 1.6–5.0 kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ a}^{-1}$  for reef flats, and greater than 2.0 kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ a}^{-1}$  for forereef environments (Hart and Kench, 2007).

### Carbonate production vs. sediment generation

Estimates of carbonate production do not equate directly to the generation of detrital sediments within coral reefs. It is commonly assumed that sediment generation is a direct function of the growth rate of reef organisms and reefs, as biological factories yield a continuous supply of sediment (Scoffin et al., 1980; Kinsey, 1985; Hubbard et al., 1990). However, this assumption is overly simplistic, as the supply of sediment involves a complex sequence of processes, dependent not only on the growth rate of organisms, but their mechanical and biological breakdown and dispersal from reef source to sink.

Secondary producers contribute directly to a reef sediment reservoir upon death, and the rate of supply is controlled by the abundance, fecundity, life cycle, and turnover of organisms. However, primary producers only yield detrital sediment following breakdown by physical and biological processes.

Physical breakdown of coral is mainly associated with extreme hydrodynamic forces exerted by storm waves, tsunami, and cyclonic wave action that exceed the mechanical strength of coral colonies (Madin, 2005). Extreme waves have been reported to disturb and break corals to water depths up to 20 m (Scoffin, 1993). Total destruction of branching corals to water depths up to 12 m has also been reported (Stoddart, 1971; Woodley

et al., 1981; Van Woesik et al., 1991). Large reef blocks more than 4-m diameter further attest to the extreme forces able to mechanically break and transport material to the reef flat surface (Scoffin, 1993).

The susceptibility of coral to mechanical damage is related to the growth form of coral colonies. Arborescent, tabulate, and spindly branched growth morphologies are the most susceptible to damage, whereas massive forms tend to be more resistant to damage (Done, 1992; Massel and Done, 1993; Madin and Connolly, 2006).

The importance of high-energy events to the sediment reservoir is the potential for the rapid generation of large volumes of detrital material within reef systems. For example, cyclone Bebe that impacted Funafuti, Tuvalu, in 1972, stripped the living coral reef on the windward side of the atoll producing  $1.4 \times 10^6 \text{ m}^3$  of detrital material which was deposited on the reef flat surface (Maragos et al., 1973; Baines et al., 1974). The geomorphic implications of such temporal pulses in sediment generation are discussed later.

Bioerosion (biological substrate erosion) also plays a major role in the conversion of reef calcium carbonate production to detrital sediment and is facilitated by a wide range of reef-associated faunas, including species of fish and echinoids, and endolithic forms of sponges, bivalves, and worms (Spencer, 1992). These biological agents directly degrade primary and secondary reef frameworks, increasing susceptibility to physical and chemical erosion. Principal modes of bioerosion include (1) destruction of loose carbonate grains through mechanical or chemical disintegration during mastication and digestion of grains and the breakage of skeletons, (2) grazing of reef framework, and (3) destruction of framework through the action of macro and microboring organisms (Scoffin, 1987; Perry and Hepburn, 2008). Bioeroding processes can produce large amounts of sediment. For example, bioerosion by echinoids and fish may contribute 0.17–9.7 and 0.02–7.62 kg  $\text{CaCO}_3 \text{ m}^2 \text{ a}^{-1}$  to the sediment reservoir, respectively, and bioerosion by sponges 0.18–3.29 kg  $\text{CaCO}_3 \text{ m}^2 \text{ a}^{-1}$  (Scoffin et al., 1980; Hubbard et al., 1990; Bruggemann et al., 1996).

In summary, the relative role and temporal variations of physical and biological processes are clearly crucial to the supply of sediment for reef platform and sedimentary landform construction. There have been a number of attempts to develop sediment budgets for reef systems. However, the majority of these studies have been interested in net reef development rather than in the detailed quantification of the detrital sediment generated on reef platforms. Notable studies that have constructed detailed sediment budgets as part of studies of reef development include the following: Stearn and Scoffin (1977) who established a sediment generation rate of 17.5 kg  $\text{m}^2 \text{ a}^{-1}$  on Bellairs fringing Reef Barbados; Hubbard et al. (1990) who established a generation rate of 0.71 kg  $\text{m}^2 \text{ a}^{-1}$  at Cane Bay fringing reef, St Croix, US Virgin Islands; and Harney and Fletcher (2003) who identified a rate of sediment generation of 0.53 kg  $\text{m}^2 \text{ a}^{-1}$



from the fringing reef at Kailua Bay, Oahu. Eakin (1996) also estimated changes in sediment production on Uva Island, Panama as a consequence of the 1982–1983 El Niño event. He showed that sediment generation changed from an estimated  $6.09 \text{ kg m}^{-2} \text{ a}^{-1}$  prior to the El Niño event to  $6.92 \text{ kg m}^{-2} \text{ a}^{-1}$  after the event as a consequence of changes in bioerosion processes.

### Characteristics of reefal sediments

The reliance on ecological processes to generate sediments in coral reef environments imparts an unique signature on the texture (size) and hydrodynamic properties of reefal sediment. Maiklem (1968) defined two textural end members resulting from the dominance of biological or physical factors. The first is an “immature” sediment, which has an inherited grain-size distribution influenced by the abundance, availability, and type of organisms present, and their size properties. Second is a “mature” sediment whose grain-size distribution is the product of hydrodynamic modification of the inherited texture. It is important to note that in most reef settings there will be a range of textural types that reflect the differential role of biological and physical processes in deposit formation.

Biological influences on sediment texture are twofold. First, they control the physical properties of skeletal grains. The nature and type of calcium carbonate secretion govern grain density, size, shape, surface texture, and skeletal microarchitecture. These properties vary significantly between the different calcium carbonate secreting organisms. For example, the density of skeletal material ranges from  $1.0 \text{ g cm}^{-3}$  for composite deposits (Chave et al., 1972) to  $2.95 \text{ g cm}^{-3}$  for the octocoral *Heliopora* (Jell et al., 1965). Second, they influence the nature of grain breakdown before, during, and after deposition. In particular, the skeletal architecture and morphology of different producers govern the size distribution of breakdown products according to the Sorby principle (Sorby, 1879; Folk and Robles, 1964). Collectively, these variations in skeletal properties influence grain durability, which depending on the mechanical force applied to skeletons is a critical control on the breakdown of carbonate sediment. Chave (1960, 1962), recently updated by Ford (2009), found that grain durability varied by several orders of magnitude from the calcareous green algae *Halimeda*, which is rapidly abraded, to coral and molluscs, which are most durable and persistent in the reef sediment reservoir. Chave (1960) also found that durability of biogenic sediment was several times less than that of siliciclastic sediment.

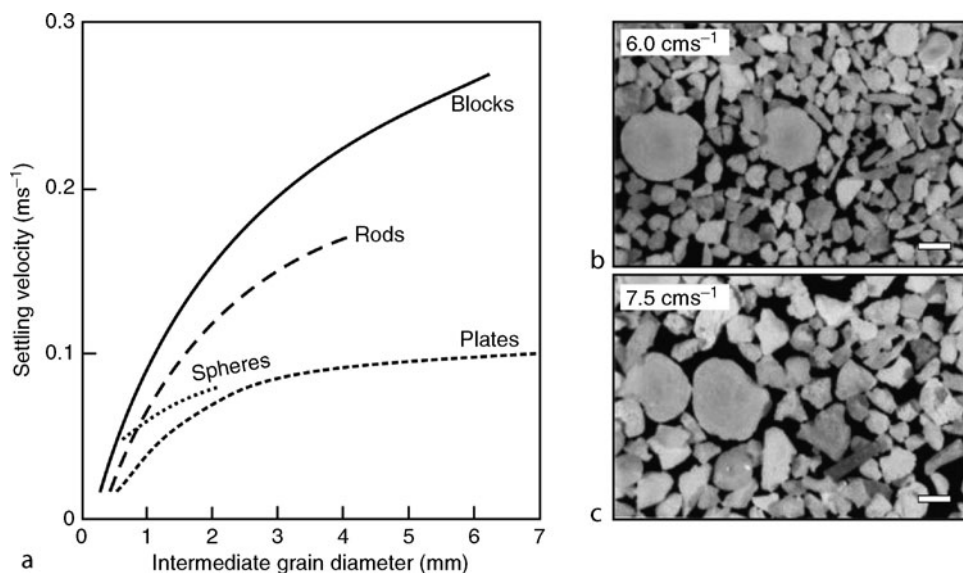
Bioerosion processes are also an important agent in the alteration of physical properties of sediments. In particular, the differing modes of bioerosion influence the size range of sediments (Milliman, 1974; Hutchings, 1986; Scoffin, 1987). For example, grazing organisms can produce coarse particles, whereas microborers produce fine sand and silt-size particles.

### Hydrodynamic properties of carbonate sediments

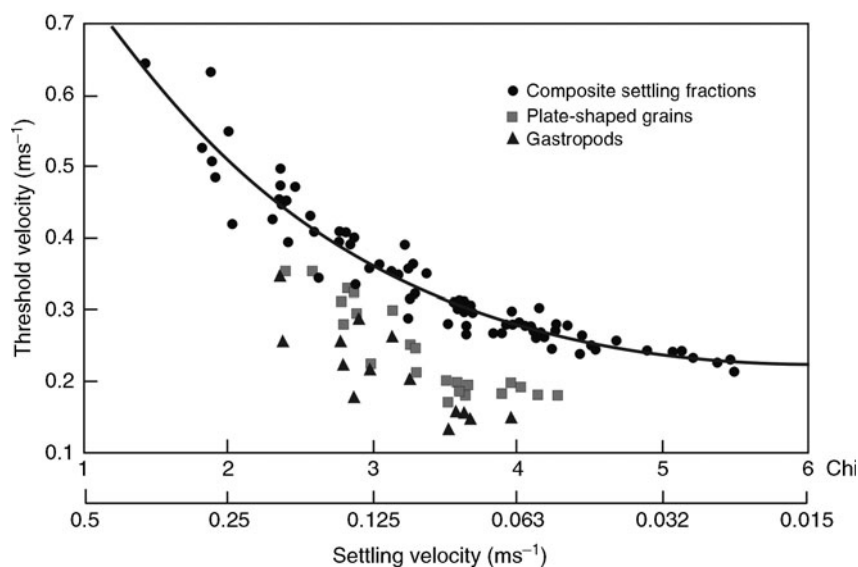
Ultimately, reefal carbonate deposits represent a heterogeneous mix of skeletal organisms, each with varying size, shape, density, and durability. These properties impart distinctive hydrodynamic properties on reefal sediments, which along with fluid flow governs the initiation of sediment movement (Scoffin, 1987; Prager et al., 1996). In general, there have been few studies of the hydrodynamic characteristics of carbonate sediments.

Conventional analyses of sediment entrainment consider grain size as the principal indicator of the hydrodynamic behavior of grains. However, a number of studies have shown that due to the heterogeneous nature of reefal deposits, mean grain size of carbonate sediments is a poor predictor of hydrodynamic performance (Maiklem, 1968; Braithwaite, 1973; Kench and McLean, 1996). Maiklem (1968) and Braithwaite (1973) identified marked differences in settling behavior of individual skeletal particles of similar size (Figure 1a). For example, plate-shaped grains (e.g., *Marginopora* sp. or *Halimeda* sp.) settle at markedly slower rates than spherical grains of equivalent diameter (Figure 1). Such findings underscore the inadequacy of adopting size as an indicator of hydrodynamic behavior and can provide misleading interpretations of sediment dynamics in coral reef environments (Orme, 1977). For example, Kench and McLean (1997) compared the measured size and measured settling behavior of samples and found that size estimates (derived from the sieve method) caused overestimation of entrainment velocities, implying that deposits were only entrained under storm conditions. However, analysis of hydrodynamic performance revealed that samples were actually able to be mobilized under fair weather wave energy conditions, indicating that the sediment reservoir was considerably more dynamic than implied by size descriptors.

Consequently, Kench and McLean (1997) and Kench (1997) adopted “settling velocity” to describe a deposit’s hydrodynamic behavior and infer sedimentation processes. Kench and McLean (1996) also undertook threshold experiments on individual constituents and composite sediment deposits to generate a threshold of entrainment relationship (Figure 2). In contrast to the generation of threshold curves based on grain size (e.g., Prager et al., 1996), results identified the velocity of entrainment of skeletal deposits and grains of known settling velocity. Results showed significant variation in entrainment potential for individual skeletal constituents with plate-shaped grains, and gastropods among the most readily entrained clasts. Of note, threshold values for composite sediments were consistent with the field-derived estimates of Hine et al. (1981). More recently, Paphitis et al. (2002) developed empirical threshold relationships for shell fragments under unidirectional flow. In this approach, thresholds are based on the hydrodynamic size of grains. In addition, Yordanova and Hohenegger (2007) have examined the hydrodynamic settling and threshold properties of larger benthic foraminifera.



**Sediment Dynamics, Figure 1** Settling properties of bioclastic sediments. (a) Settling behavior of common bioclastic shapes (after Maiklem, 1968). (b, c) Photomicrographs of bioclastic grains with equivalent settling values from Kench and McLean (1996). Settling velocity values shown in brackets. Note the varied size, shape, and constituent mix of settled fractions. Scale bar = 1 mm.



**Sediment Dynamics, Figure 2** Threshold velocity vs. mean settling velocity of composite bioclastic sediment fractions and individual bioclastic constituents. Measured velocities 0.025 m above sediment surface. After Kench and McLean (1996).

### Controls on sediment entrainment, transport, and deposition

The entrainment and dispersal of sediment on and adjacent to coral reefs is controlled by hydrodynamic processes and moderated by a number of biological processes. Instantaneous wave-induced currents are the primary mechanism for the entrainment of sediment in reef systems. In general, maximum wave-induced forces occur toward the edge of

reef platforms where wave breaking occurs, and these forces diminish across the reef as wave energy is dissipated (Roberts et al., 1992; Brander et al., 2004). Consequently, spatial and temporal gradients in the entrainment potential of sediments exist in reef systems. Such variations are predictable as tidal modulation of water level across reefs controls the temporal window within which gravity wave energy can propagate onto reef

flats. As water depth over reefs increases, a greater proportion of incident wave energy can leak onto reef flats, and in some instances, at highest tidal levels, waves propagate across the reef edge without breaking (Brander et al., 2004; Kench et al., 2009a). Water depth across reefs also controls the maximum height of reformed waves on a reef flat (Gourlay, 1994; Nelson, 1994; Hardy and Young, 1996) and, therefore, the boundary stresses available to entrain sediments. Hardy and Young (1996) found that the upper boundary of significant and maximum wave heights is limited to less than 40% and 60% of the reef flat water depth, respectively.

These temporal and spatial variations in wave energy have significance for modulating timeframes of sediment entrainment on coral reefs. Kench and Brander (2006a) introduced the *reef energy window index* to account for these variations. The index identifies the temporal window within which gravity wave energy can propagate onto reefs and stimulate sediment entrainment, a function of reef width, water depth over reefs, and incident wave conditions. In general, the index predicts that sediment transport is activated for longer periods on reefs that have small width and higher relative water depths (Kench and Brander, 2006a). Wide reefs and shallow water depths are characterized by short temporal windows within which the sediment transport system can be activated. For example, Brander et al. (2004) show that due to the elevated nature and broad width of the Warraber reef flat in Torres strait the sediment transport system is activated for only 1–2 h around high tide.

Once entrained, wave and tide-induced currents are able to transport sediment within reef systems. The rate of transport is governed by the current magnitude and settling velocity of particles. The direction of transport is largely controlled by the net and residual current flows within reef systems. The pathways and rates of sediment movement are of critical importance for the development of sedimentary landforms.

Biological agents are able to modify entrainment and depositional processes. Benthic organisms are able to preferentially entrain, disperse, and sort sediments (Scoffin, 1987). In particular, bioturbating organisms have been found to enhance transport by expelling sediment into the water column (Roberts et al., 1981; Frith, 1983) and thus are important in zones where hydrodynamic energy is insufficient to entrain sediment. de Vaugelas (1985a, b) and Tudhope and Scoffin (1984) show that bioturbation is also able to obliterate primary sediment textures through preferential sorting of finer grain sizes and the vertical mixing of sediment within the top 1.0 m of the sediment body.

In contrast, biological and chemical processes can play an active role in the deposition and stabilization of sediment and can have a strong influence on sediment texture. Seagrasses have the ability to baffle flow, inducing deposition of material, and bind sediment within root systems (Ginsburg and Lowenstam, 1958; Sellwood, 1986).

Neumann et al. (1970) found that the binding effect of seagrass and other flora significantly increased the threshold required to entrain sediment. In addition, a number of other mechanisms act to bind and stabilize sediments, which also raises the effective sediment thresholds. Such processes include physicochemical and organically induced precipitation of aragonite and Mg calcite crystals around grains to produce aggregates and cemented rocks, pelletization of sediment-ingesting organisms (e.g., Holothuria), and binding by algal mats (Scoffin, 1987).

### Sediment transport studies

A detailed understanding of sediment dynamics is important to better resolve depositional patterns in reef environments, predicting changes in sediment fluxes and reef-associated sedimentary landforms as a consequence of environmental change, and understanding the long-term evolution of geomorphic features on coral reefs. Furthermore, analysis of sediment transport pathways, rates of sediment transport, and process mechanisms driving transport are fundamental to support contemporary management of reef-associated sedimentary landforms and sediment resources, which are increasingly targeted as sources of aggregate by communities in coral reef settings (e.g., Brown and Dunne, 1988).

### Quantitative studies of contemporary sediment dynamics

There have been very few quantitative observations of sediment transport and the process mechanisms controlling transport processes in coral reef environments. In part, this is due to the practical difficulties of undertaking such measurements and the spatial and temporal variability in sediment transport in coral reef environments. Common approaches to establish sediment transport rates include sediment trapping, tracing tagged sediments, and more recently optical and acoustic sensor technologies.

Sediment transport pathways and rates of movement on fringing and forereef environments have been the focus of a number of studies, which have highlighted the off-reef flux of sediment. Hughes (1999) showed the downslope movement of larger clasts to talus slopes at Lizard Island, Great Barrier Reef. In the Caribbean, a number of studies have examined transport patterns, with many establishing off-reef transport that is responsible for development of large sand deposits (Meaney, 1973; Clack and Mountjoy, 1977; Hine et al., 1981; Land, 1979; Sadd, 1984; Hubbard, 1986; Hubbard et al., 1981). Using sediment tracers, Hubbard et al. (1990) showed that rates of sediment transport varied from average values of  $112 \text{ kg m}^{-1}$  under fair-weather conditions to  $745 \text{ kg m}^{-1}$  under storm conditions with an estimated total off-reef sediment transport of  $55,100 \text{ kg a}^{-1}$ .

A small number of studies have examined sediment transport patterns on reef flats around reef islands in the Great Barrier Reef (e.g., Flood, 1974; Hopley, 1981; Gourlay and Jell, 1993). Similarly, there have been few



attempts to quantify contemporary sediment transport rates in atoll systems. Guppy (1889) produced one of the earliest detrital sediment transport budgets from the Cocos (Keeling) atoll, Indian Ocean. Based on sediment trap data, Guppy estimated that  $1,500 \times 10^3 \text{ kg a}^{-1}$  of sediment was transported from ocean reef flats to shallow lagoon. Kench (1998a) and Kench and McLean (2004) reassessed this budget based on sediment fluxes through the shallow interisland channels on the atoll reef rim. Their data showed that significant differences in channel sediment transport occurred as a consequence of the reef width and hydrodynamic processes. On the high energy eastern side of the atoll, narrow reef widths and wave propagation onto the reef flat activated the transport system under fair-weather conditions and was efficient in transferring sediment through eastern channels at rates of  $268 \text{ kg day}^{-1}$ . The transport potential of these channels was limited by the supply of sediment. In contrast, broad reef flats (1.5 km) on the southern atoll acted to effectively dissipate wave energy. Consequently, the transport system was inactive under fair-weather conditions, with transport rates of  $\sim 2.2 \text{ kg day}^{-1}$ , and sediment accumulated in situ on reef flats. These channels were limited by the energy available to activate transport. However, under storm conditions higher wave energy propagated onto these reef flats and activated the transport system. Of note, measurements undertaken during a cyclone showed that sediment transport increased to 4,100 and 5,155  $\text{kg day}^{-1}$  through eastern and southern channels, respectively.

The majority of the above studies are site-specific case studies that have focused on bedload fluxes of sediment within coral reefs, which principally involves movement of sediments in the sand and gravel size range. These studies all show that transport is active under fair-weather conditions but can be substantially enhanced under higher energy (storm/cyclone) conditions.

A number of studies have also examined the fluxes and process mechanisms controlling suspended sediment fluxes in fringing, barrier, and platform reef systems (e.g., Davies and West, 1981; Orpin et al., 1999; Hoitink and Hoekstra, 2003). In particular, these studies have focused on the behavior of terrigenous inputs to reefs systems as they can pose severe ecological threats to reefs (e.g., Brodie and Furnas, 1996). Specific threats include reduction in photosynthetically active radiation (PAR), abrasion by sediment, reduction in hard substrate, and smothering by corals (Rogers, 1990; Fabricus and Wolanski, 2000; Dollar and Grigg, 2004). Recent investigations of suspended sediment fluxes have utilized high temporal resolution monitoring equipment that sample at the same rate as hydrodynamic measurements and allow long and continuous datasets to be obtained. Examples of such studies include Storlazzi et al. (2004) and Presto et al. (2006) on the fringing reef of southern Molokai, Hawaii; Orpin et al. (1999) in the Great Barrier Reef lagoon; and Hoitink and Hoekstra (2003) in Indonesia. Collectively, results from these investigations show that

fine sediments can be suspended under fair-weather conditions on reefs and in lagoons, net transport is a function of net current direction, fine sediments are effectively flushed from high-energy reef settings but aggregate in lower energy reef and lagoon environments, and that the orientation of the coast with respect to prevailing winds and waves is an important determinant on whether sediment is trapped or flushed from a reef system.

### Sedimentological interpretation of sediment dynamics

In lieu of detailed sediment transport measurements, interpretations of sediment transport and deposition in carbonate settings have been based on textural and skeletal component analysis (McKee et al., 1959; Folk and Robles, 1964; Flood et al., 1978; Wardlaw et al., 1992; Smithers et al., 1994; Randazzo and Baisley, 1995); broad (reef-wide) tide- and wave-driven current processes (Suhayda and Roberts, 1977; Flood and Scoffin, 1978; Hubbard et al., 1981; Lugo-Fernandez et al., 1994); and limestone classifications in which sediment size, skeletal constituents, and surrounding matrix are used to reflect the interaction of biological and hydrodynamic processes (Folk, 1962; Dunham, 1962; Tucker and Wright, 1990). Problems have been identified with these approaches, which have been attributed to the unique character of coral reef sediment systems and conventional tools used to characterize carbonate deposits (Orme, 1977; Scoffin, 1987).

Unlike siliciclastic environments, where production, transport, and depositional zones are commonly spatially and temporally separated, carbonate sediment is normally produced within the basin of deposition (Ham and Pray, 1962). There are a number of implications of this for interpretation of sediment deposits. First, zones of sediment production and deposition may be closely associated or overlap. Second, deposits may accumulate in situ with little influence from the hydrodynamic process regime. Therefore, the texture of such "death assemblages" has no relationship to the hydrodynamic regime. As a consequence the intrabasinal provenance of reefal sediment, together with the heterogeneous character of biogenic deposits, presents significant difficulty in the interpretation of sedimentation and sediment transport processes (Scoffin, 1992; Tucker and Wright, 1990).

An additional factor impeding the interpretation of sediment transport processes in reef environments results from the standard approach for analysis of carbonate sediment texture (Orme, 1977; Scoffin, 1987; Kench and McLean, 1996). Conventional grain-size distributions (derived from mechanical sieving) are unable to differentiate the relative importance of physical and biological processes in deposit formation (Orme, 1977; Kench, 1998b). Furthermore, as noted earlier, mechanically derived size distributions do not reflect the hydrodynamic characteristics of heterogeneous carbonate deposits.

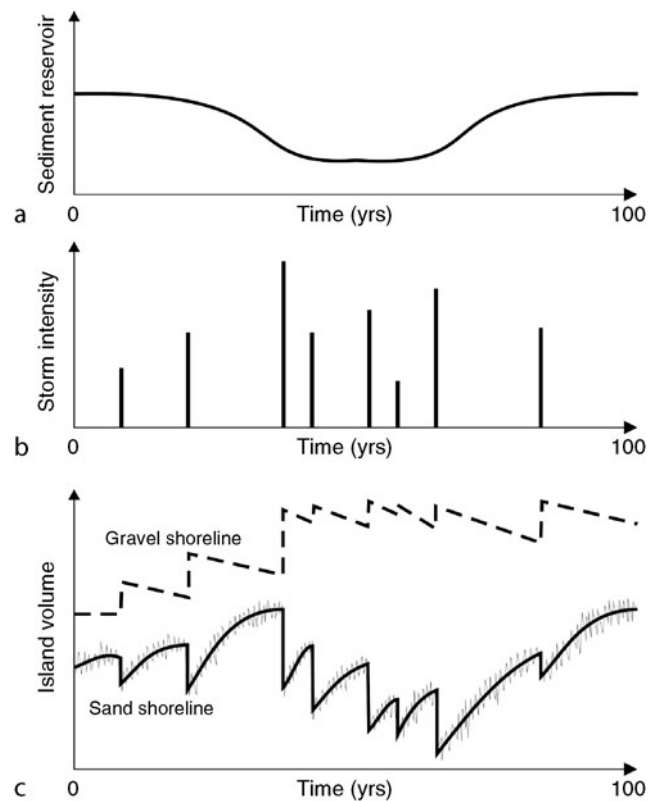
Orme (1977) and Scoffin (1987) recognized these constraints and proposed that a “currents of removal” approach would provide a more powerful approach for interpreting deposit formation. A currents of removal approach was developed by Kench (1998b), which combined the hydrodynamic properties of sediments with measurements of wave energy to model the mobile portions of sediments. Such an approach enables the mobile and nonmobile fractions of deposits to be isolated and provides improved resolution of transport pathways in reef systems and the relative importance of transport and local sediment production processes in deposit formation.

The detection of sediment transport pathways in coral reefs has also been approached through the use of key skeletal constituents as sediment tracers. In this approach, organisms with known restricted production zones are used to reconstruct pathways of sediment movement based on both gradients in concentration of tracer constituents and the predictable taphonomic alteration of constituents in deposits. Examples include the use of the depth zonation of different species of *Halimeda* to infer off-reef transport at Grand Cayman Island, West Indies (Johns and Moore, 1981); foraminifera of known settling velocity to construct reef to lagoon transport pathways in the Cocos (Keeling) Islands, Indian Ocean (Kench, 1997) and the known taphonomic breakdown of the foraminifer *Baculogypsina* to construct transport patterns on Lizard Island fringing reef, Great Barrier Reef (Ford, 2009).

### Dynamics of sedimentary landforms

In general, studies of contemporary sediment transport processes in coral reefs have focused on short timescales (seconds to days), small spatial scales (point measurements), and examined pathways of transport. However, significant insights into sediment dynamics in reef systems can also be gained through examination of volumetric changes in sediment stores (e.g., reef islands, sand aprons) as expressed through morphological change. Typical morphological adjustments include shoreline erosion, accretion, sediment wash over, shoreline realignment, and island migration (Kench et al., 2009b). The major process controls on the formation and stability of reef sedimentary landforms are sediment supply and oceanographic regime. Wave action and its interaction with the coral reef surface determine current and sediment transport patterns that ultimately control the location of sediment deposition (Gourlay, 1988; Kench and Brander 2006a). Such processes are modulated by climate, and consequently, reef landforms exhibit rapid morphological adjustment to changes in these incident processes at a range of timescales.

At event scales, storms and hurricanes have both constructional and erosional impacts on reef sedimentary landforms (Figure 3). These contrasting responses reflect differences in storm frequency and texture of island-building materials (Bayliss-Smith, 1988). In settings with low storm frequency landforms are typically composed of sand-size sediments, which are susceptible to erosion



**Sediment Dynamics, Figure 3** Temporal variations in sediment storage and morphological change in reef islands: (a) Medium-term changes in sediment supply and (b) storm frequency and intensity leading to (c) a conceptual model of reef-associated landform response. Note: grey line in (c) depicts short-term shoreline morphodynamics. After Kench et al. (2009a, b).

during extreme events. Stoddart (1963) reported mass destruction of some reef top islands in Belize as a result of Hurricane Hattie, which depleted the island sediment reservoir. Kench et al. (2006, 2008) examined the morphological adjustments of Maldivian reef island sediment stores in response to the December 2004 Sumatran tsunami. They found that reef islands experienced erosion of shorelines by up to 9% of island area, overwash sedimentation which contributed up to 1,200 m<sup>3</sup> to island surfaces, lateral extension of beaches across reef flats, and evidence of off-reef transport down forereef sand chutes. Collectively, these observations indicated that the tsunami promoted exchange of sediment between the different sediment stores on the reef platform.

In contrast, in reef settings with high storm frequency islands are commonly composed of rubble on their exposed margins, while leeward and fringing reef-fronted coastal plains are composed of sand-size material. In such settings, large volumes of rubble can be generated in single events from coral communities on the outer reef. As noted earlier, Hurricane Bebe (1972) deposited  $1.4 \times 10^6$  m<sup>3</sup> of rubble as a rampart on the reef flat and islands of Funafuti Atoll, Tuvalu (Maragos et al., 1973).

Subsequent storms have reworked this rampart onto island shorelines, showing that the hurricane and subsequent storm processes added approximately 10% to island area (Baines and McLean, 1976). Sequential deposition of rubble ridges has also been identified in the late Holocene evolution of gravel islands in the Great Barrier Reef (Chivas et al., 1986; Hayne and Chappell, 2001).

At seasonal scales, Kench and Brander (2006b) examined the morphological sensitivity of 13 islands in the Maldives to predictable changes in wind and wave conditions controlled by the oscillating monsoons. Results identified rapid, seasonal morphological adjustments of island shorelines (up to 53 m of beach change) equating to 20,000 m<sup>3</sup> of sediment movement between seasons, despite morphological near-equilibrium on an annual basis. However, the magnitude of morphological change (sediment flux), and sensitivity of islands to change, were found to vary between islands as a function of reef platform shape, which controls wave refraction patterns.

At the decadal scale, shifts in prevailing wind fields and their influence on wave propagation (direction and energy) control erosion and accretion patterns on reef islands resulting in island migration (e.g., Verstappen, 1954; Flood, 1986). The Pacific decadal oscillation (PDO) and its effect on modulating storm frequency have been found to control multidecadal fluctuations in longshore sediment transport, resulting in erosion and accretion patterns of  $\pm 100$  m on the Kihei fringing reef shoreline, Maui (Rooney and Fletcher, 2005). Interannual El Niño Southern Oscillation (ENSO) variations have also been implicated in shoreline erosion and accretion patterns in Kiribati (Solomon and Forbes, 1999).

Variations in sediment supply either through changes in sediment generation on the reef flat or in net littoral transport gradients also exert a further control on landform change at medium to long timescales (e.g., Figure 3). However, while the role of process-driven changes on the sediment budget is somewhat predictable (Rooney and Fletcher, 2005; Kench et al., 2008), temporal variations in sediment generation of suitable grade for landform development and their influence on reef landform dynamics are poorly understood.

Differences and changes in accumulation history of reef sedimentary units at geological timescales may be explained through temporal variations in sediment supply and recognition that the relationship between reef carbonate productivity and sediment generation is nonlinear. For example, variations in sediment supply are likely to reflect shifts in the balance between reef growth and reef productivity for both primary and secondary sediment producers. During rapid catch-up growth mode, the reef structure was effective at retaining calcified products in the reef framework. However, as reefs reached wave base and vertical growth was constrained, excess carbonate was shed from the reef system and was either exported from the reef or made available for construction of sedimentary deposits. Consequently, the general trend for studies to identify the onset of development of sedimentary features (islands

and sand aprons) in the mid-Holocene (e.g., Woodroffe et al., 1999; Smithers et al., 1994; Harney et al., 2000; Woodroffe, 2003) may coincide with reefs either reaching sea level or reaching wave base and releasing a pulse of excess sediment for landform construction. In many reef settings, this may have coincided not only with a transition from vertical to lateral reef growth but also to reef flat emergence, which may have promoted shifts in reef flat ecology and thus carbonate production. As a consequence, the dominant constituents available for accumulation of sedimentary units may have shifted from sediments derived from frame builders (coral and coralline algae) to those derived from other sediment producers (e.g., foraminifera, calcareous green algae). Yamano et al. (2000) identified such ecological change, to a foraminifera-dominant reef platform following sea level stabilization at Green Island, as a key trigger for the onset of island formation and development. Similar reliance for island building on a narrow range of skeletal constituents has been identified by Woodroffe and Morrison (2001) in Makin Island, Kiribati.

The accumulation history of reef islands has also shown considerable variation in response to sediment supply. For example, on Warraber Island in the Torres Strait, island development has occurred incrementally over the past 3,000–5,000 years in response to continued supply of sediment (Woodroffe et al., 2007). At Hanalei Bay, Hawaii, Calhoun and Fletcher (1996) identified a gradual reduction in the rate of coastal progradation during the Holocene controlled by declining sediment supply. In contrast, Maldivian reef islands appear to have formed (primarily of *Halimeda*) in a 1,500-year window in the mid-Holocene and effectively ceased accumulation 3,500 years ago (Kench et al., 2005). Episodic land accumulation has also been identified in storm-dominated settings where reef development and island building have occurred in discrete depositional phases of storm-derived rubble (Maragos et al., 1973; Bayliss-Smith, 1988; Blanchon and Jones, 1997; Blanchon et al., 1997; Hubbard, 1997; Hayne and Chappell, 2001).

The reliance of some landforms on a select number of skeletal constituents also suggests that sediment availability through the late Holocene is also likely to have been influenced by biological perturbations (infestations of bioeroding organisms or mass death of secondary producers) that release pulses of sediment to the reef system and influence phases of deposition in sediment stores on reef systems. Consideration of the importance of sediment supply to reef sedimentary landforms highlights a number of issues fundamental to understanding morphological change and fluxes of sediment in storage zones within reef systems. It is commonly assumed that the reef “carbonate factory” produces a quasi-continual supply of sediment to build or maintain landforms. However, existing studies suggest that both the supply and composition of sediments available for land building can vary temporally in response to changes in reef growth/reef ecology (Yamano et al., 2000; Woodroffe, 2003), and these in turn influence



the accumulation behavior of reef sedimentary units. However, scientific understanding of the processes that “turn on” and “turn off” sediment supply as it relates to the construction of these sedimentary stores (islands, sand aprons) is poor. Exploratory modeling studies suggest that changes in sediment supply, either through alterations in sediment generation or littoral budgets, may be more important than sea level in affecting the stability of reef sedimentary landforms (Kench and Cowell, 2003; Woodroffe, 2003).

## Summary

The dynamics of carbonate sediment systems are controlled by the interaction of biological and physical processes that interact at a range of space and timescales to generate sediment, transfer sediment within reef systems, and form a suite of different sedimentary units within coral reefs. A large body of research exists on aspects of coral reef sedimentation including  $\text{CaCO}_3$  production, descriptions of carbonate sediment deposits and facies, and the geological development of coral reef platforms as sedimentary units. However, significant gaps exist in scientific understanding of the contemporary dynamics of carbonate sediments. Few studies have attempted to quantify the rate at which detrital sediment is produced in reef systems or the temporal variations in sediment generation. Furthermore, the physical process controls on the dispersal and deposition of carbonate sediments and the rates of sediment transport in modern coral reefs are also poorly resolved with field-based studies limited to only a few sites. Collectively, an improved understanding of contemporary sediment generation and transport processes is fundamental for understanding the controls on the development and morphological dynamics of sedimentary deposits in coral reefs.

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## Cross-references

[Bioerosion](#)  
[Carbonate Budgets and Reef Framework Accumulation](#)  
[Cay Formation](#)  
[Eco-Morphodynamics](#)  
[Halimeda](#)  
[Reef Flats](#)  
[Sediments, Properties](#)  
[Sediment Durability](#)  
[Tropical Cyclone/Hurricane](#)

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## SEDIMENTS, PROPERTIES

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## Definition

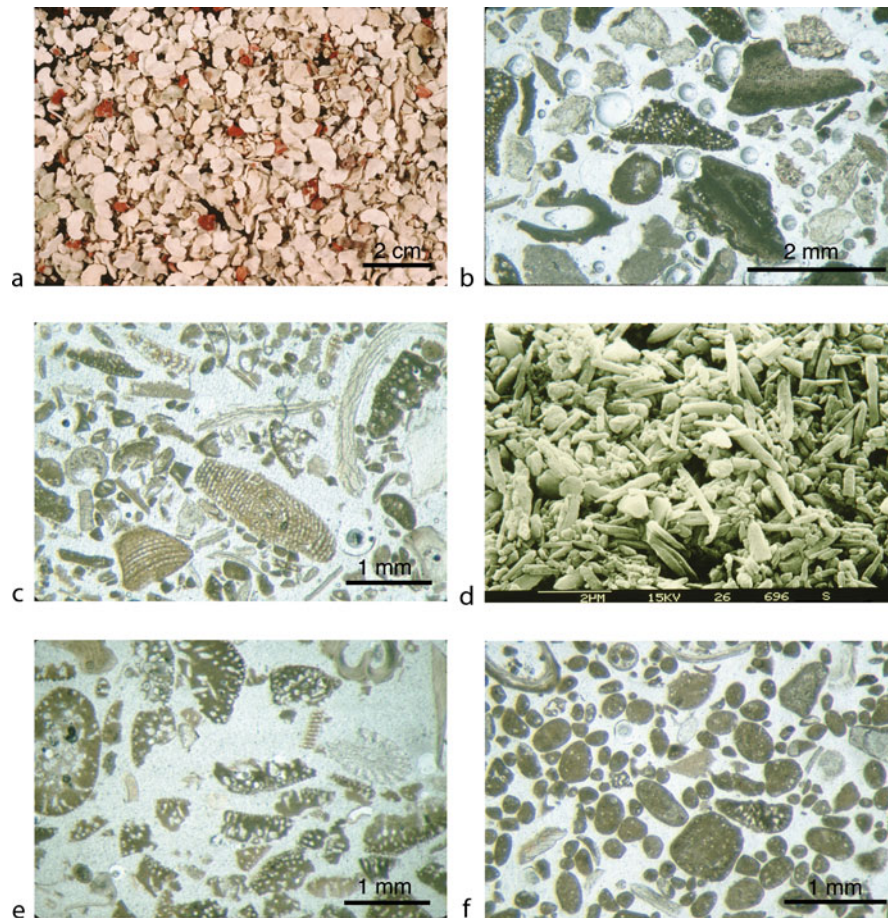
Together with the reef framework and carbonate cements, reef sediments contribute to the accretion of a coral reef. Scoffin (1992) reviewed the various contemporaneously occurring processes such as framework construction, reef

destruction (physical and biological), sediment transport and redeposition, and cementation, which eventually produce a reef limestone. Reef sediment composition and texture are also an expression of reef ecology, because the producers of reef sediments are largely reef-dwelling, carbonate-producing organisms.

### Composition

Carbonate-secreting organisms, the shells and skeletons of which eventually end up in reef sediments include Scleractinian corals, green (*Halimeda*, *Penicillus*) and red calcareous algae, mollusks, foraminifera, and echinoderms. Fragments of sponge, tunicate, or octocoral spicules, brachiopod shells, bryozoa, serpulids, and crustacean carapaces also occur but are volumetrically unimportant. Tests of pelagic organisms such as planktonic foraminifera and coccoliths may also be found occasionally in low quantities in reefal sediments. Usually, marginal reef sediment is dominated by fragments of coral

skeletons, red coralline algae, and *Halimeda* (Figure 1a and b). Mollusk shells and foraminifer test are less common. Lagoonal or platform interior sediments normally have high abundances of mollusk and foraminiferal shell fragments, with coral, coralline algae, and *Halimeda* occurring in lower abundances (Figure 1c). The classic study of Ginsburg (1956) in south Florida exemplifies these findings. A number of sediment distribution maps of major reef systems were compiled by Ginsburg and James (1974). Interestingly, all major barrier reef systems such as Australia, Belize, Florida, or New Caledonia are characterized by the terrestrial input and offshore intermixing of siliciclastic into carbonate sediments. The fine grain-size fraction ("mud") of lagoonal sediment is often composed of large parts of aragonite needles and nanograins originating from codiacean algae such as *Penicillus* (Stockman et al., 1967) (Figure 1d). *Halimeda* platelets appear to be especially abundant in restricted Caribbean reef lagoons (Gischler and Lomando, 1999),



**Sediments, Properties, Figure 1** Photograph of reefal sediments from Belize. (a) Marginal reef sand with fragments of *Halimeda*, coral, coralline algae, mollusks, forams (*Homotrema*), and echinoderms. (b) Thin-section micrograph of same sample. (c) Micrograph of lagoonal sediment with mollusk, foraminifer, and *Halimeda* fragments. (d) SEM-micrograph of carbonate mud from Belize atoll lagoon with codiacean aragonite needles and nanograins. (e) *Halimeda*-rich sediment from restricted Turneffe Islands lagoon. (f) Shallow lagoonal sediment with abundant nonskeletal grains (peloids).

(Figure 1e). In addition, nonskeletal grains such as ooids, peloids, and aggregate grains (grapestones, lumps) are found in a number of Caribbean and Indo-Pacific reef lagoons and carbonate platforms (Figure 1f). Peloids include ellipsoidal cemented fecal pellets, mud clasts, or micritized and rounded skeletal grains. Nonskeletal grains form in environments that are characterized by comparatively low sedimentation rates and where carbonate precipitation/cementation is favored (high temperature, elevated salinity, shallow and agitated water). According to Millman (1969), there is a fundamental difference between Atlantic and Indo-Pacific reef sediments in that nonskeletal grains are only abundant in the Caribbean. This author explained the difference, which he termed the “ooid problem,” by the lower depths of Caribbean as compared to Indo-Pacific reef lagoons. Exchange-rates of carbonate-rich waters that potentially lead to cementation and/or precipitation of nonskeletal grains are much higher in Caribbean lagoons (days) than in Indo-Pacific lagoons (weeks-months). However, the recent discovery of abundant non-skeletal grains in Indo-Pacific reefs (Braithwaite, 1994; Rankey and Reeder, 2009; Gischler, 2010) challenges this concept. More data on sediment occurrence and distribution are needed, especially from the >300 atolls in the Pacific Ocean. Characteristics of the various skeletal and nonskeletal grains are not discussed here. Detailed descriptions may be found in a number of standard textbooks (e.g., Millman, 1974; Tucker and Wright, 1990; Flügel, 2004).

### Texture

Unlike in siliciclastic sediments, grain-size analyses including the interpretation of means, medians, sorting, skewness, and kurtosis of reef sediments are only of limited environmental significance (Scoffin, 1992). First, the morphology and micro-architecture of carbonate grains determines the grain-size distributions of the breakdown products (“Sorby Principle”) (Figure 2). Second, the hydraulic characteristics of carbonate grains of the same size may be significantly different based on micro-architecture. For example, a bivalve mollusk shell fragment is much denser as compared to a coral fragment of the same size. Third, the way carbonate grains are broken down will also determine the resulting grain-size. Particle breakdown can be caused either by physical or biological agents. Biological breakdown in turn can occur in a number of ways, for example, by fish, by boring sponges and mollusks, or by bacteria. Fourth, the rate of carbonate production is decisive in that high-productivity environments are characterized by coarser grain-sizes as compared to places where the rate of carbonate production is low, particles are exposed to abrasion for a longer time period, and the resulting sediment is finer grained. Fifth, bioturbation, such as the intensive burrowing of callianassid shrimps in reef lagoons may fundamentally alter grain-size distribution in the upper meter of the sediment column. Sixth, trapping and binding in seagrass beds

or microbial mats in reef lagoons may lead to the accumulation of fine-grained sediment in areas where currents are comparably high. Because the traces of seagrass meadows and microbial mats are usually lost shortly after burial, fine grain-sizes may be found in high energy environments. Indeed, correlations between water depth and sediment grain-size in reefs is often statistically not significant. Still, there are rules of thumb in that, for example, marginal reef sediments contain lower volumes of fines than lagoonal sediments (e.g., Ginsburg, 1956). In order to be able to compare modern and ancient reef facies, some authors have used the Dunham (1962) nomenclature for reef sediment distribution maps even though the nomenclature was designed for rocks (e.g., Enos, 1974; Gischler and Lomando, 1999).

### The mud problem

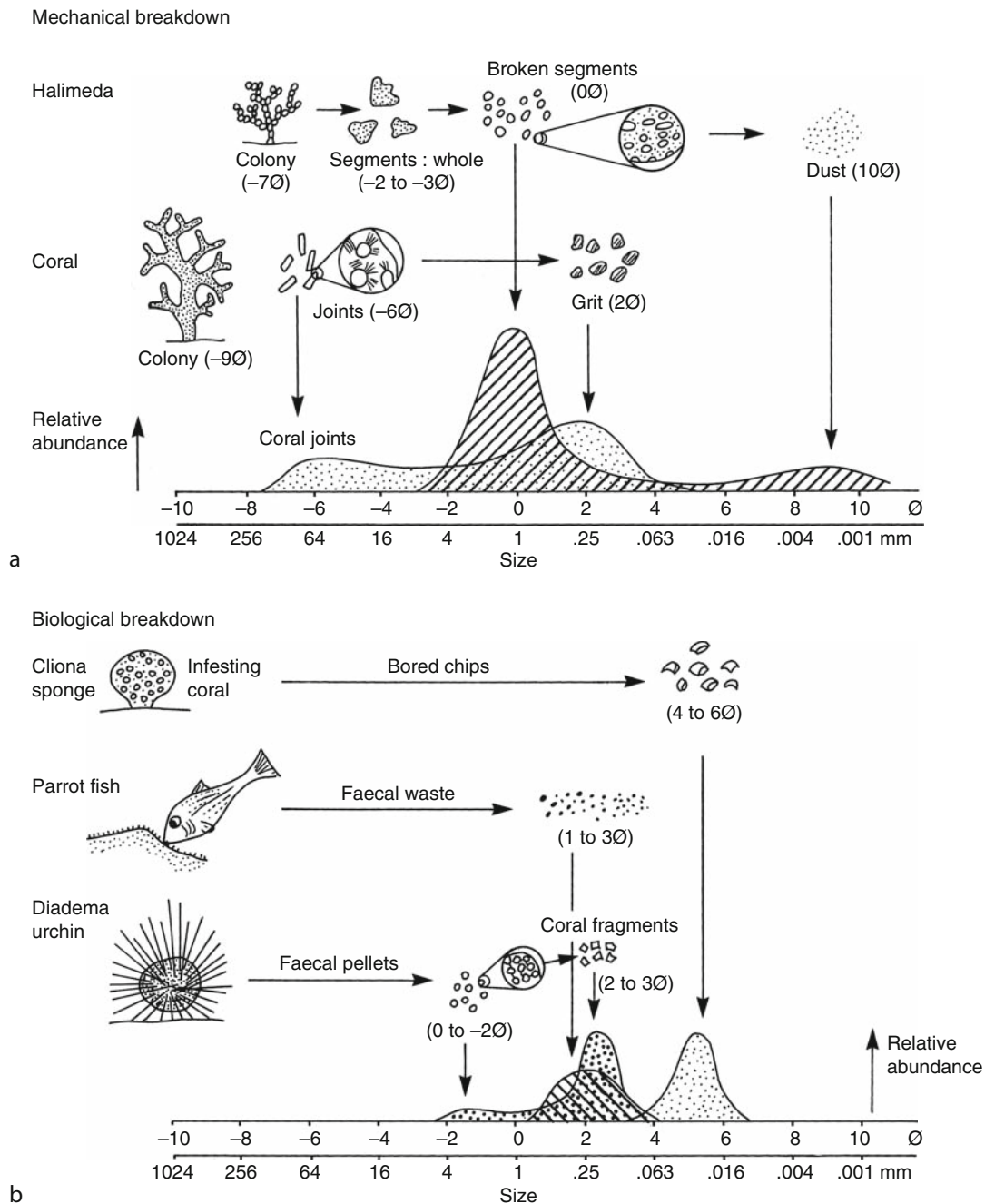
In reef sediment studies, the composition of the grain-size fraction >125  $\mu\text{m}$  or >63  $\mu\text{m}$  is usually investigated using standard light microscopes. The composition of the grain-sized fraction <63  $\mu\text{m}$  (“mud”) is normally not included in quantitative analyses. The origin of mud has to be identified under SEM. Numerous studies in Atlantic, Indian, and Pacific Oceans have shown that lagoonal muds are largely of biogenic origin, that is, consist of very small skeletal grains and grain fragments (Stockman et al., 1967; Adjas et al., 1990; Gischler and Zingeler, 2002; Gischler, 2006). The ongoing controversy regarding the origin of carbonate mud largely concentrates on the Bahamas platforms. There, evidence for direct (codiacean aragonite needles) and indirect (bacteria) biological origin, inorganic aragonite precipitation, or combinations of both are considered (see, for example, discussion in Gischler and Zingeler, 2002).

In addition, the occurrence of whittings, suspensions of aragonite crystals and seawater are controversially discussed as expressions of spontaneous carbonate precipitation in the water column or resuspended sediment (e.g., Robbins et al., 1997; Broecker et al., 2000). An interesting new aspect was recently added to the discussion by Macintyre and Aronson (2006) who found evidence for high magnesium calcite precipitation in lagoonal waters of Belizian and Panamanian reefs.

### Sediment alteration

Physical breakdown of sediment grains predominates in marginal reef settings, whereas biologic breakdown including microboring is more important in lagoonal settings (Swinchatt, 1965; Perry, 2000). In general, sediment in marginal reef areas is exposed to taphonomic alteration for much shorter time periods as compared to lagoonal sediment, which is prone to slow consolidation, biological reworking (e.g., by callianassid crustaceans), recrystallization, and even dissolution (Perry, 1996). Reid and Macintyre (1998) show that numerous skeletal grain types in reefs and carbonate platforms are diagenetically altered in very early stages. For example, the aragonitic *Halimeda* plates start to recrystallize when the alga is





**Sediments, Properties, Figure 2** Grain-sizes produced by breakdown of carbonate grains in reefal sediments (from Scoffin, 1992).

still living. A further typical alteration of reef sediment is the development of micrite envelopes (Reid and Macintyre, 2000). They form due to the activity of microborers, which leave a network of small peripheral cavities that are subsequently filled by the precipitation of microcrystalline cement or fibrous aragonite. These grains are sometimes also referred to as cortoids. In case of complete micritization of grains, peloids may form (see above).

### Aspects of reef sediment dynamics

Gross production of calcium carbonate is highest in reef areas of high cover of corals and algae such as the marginal reef and fore reef environments. It is generally lowest in the back reef environments and intermediate in lagoonal coral patch reefs (Chave et al., 1972). Studies of sediment cycling in reefs have shown that the net production, that is, the amount of calcium carbonate retained in the reef as sediment and framework, may be

significantly lower than gross production as sediment tends to be exported to the fore reef and to deep water (Land, 1979; Hubbard et al., 1990). According to the excellent study of Hubbard et al. (1990), reefal carbonate production in a Caribbean reef system ranged from 0 to 5.78 kg  $\text{CaCO}_3/\text{m}^2/\text{year}$ , with a reef-wide average of 1.21 kg  $\text{CaCO}_3/\text{m}^2/\text{year}$ . Of this gross production, 0.91 kg  $\text{CaCO}_3/\text{m}^2/\text{year}$  remained in the reef whereas the missing 0.3 kg  $\text{CaCO}_3/\text{m}^2/\text{year}$  is lost from the reef. In some studies, radiometric ages (Maxwell, 1969; Gischler and Lomando, 2000) or combined  $^{14}\text{C}$  and  $^{210}\text{Pb}$  radioisotopes (Walbran, 1996) from reef sediments were used in order to decipher sediment dynamics and reworking, respectively. Li et al. (1997) successfully used grain-size distributions of foraminiferal tests in modern sediment samples in order to trace sediment redeposition within the fringing reefs of Grand Cayman.

## Summary

Reef sediments are largely composed of the shells and skeletons, as well as shell and skeleton fragments of carbonate-secreting organisms (skeletal grains). The most abundant include Scleractinian corals, Codiacean algae, red coralline algae, bivalve and gastropod mollusks, and benthic foraminifera. Nonskeletal grains such as ooids, peloids, and aggregates reach elevated abundances in some shallow lagoon and platform areas. Grain-sizes range from mud to rubble and boulders. Sand sizes are common on reef margins. Carbonate mud in reef lagoons is largely of biogenic origin; only the muds of the Bahamas appear to originate predominantly from physicochemical carbonate precipitation. Reef sediments are usually altered biologically and/or physically by breakage, boring, burrowing, encrustation, cementation, recrystallization, and dissolution. Carbonate production in reef amounts to several kg  $\text{CaCO}_3/\text{m}^2/\text{year}$  on average. Considerable amounts of carbonate sediments are exported from reefs and do not get incorporated in the framework.

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## Cross-references

Bioerosion

Diagenesis

Holocene Reefs: Thickness and Characteristics

Sediment Dynamics

## SEISMIC REFLECTION

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## Synonyms

Seismic mounds or buildups; Seismic reef; Seismic reef sedimentology

## Definition

Seismic reef – reflected elastic wave image of the sedimentary architecture of a reef geomorphic body, and the expression of karst at significant subaerial surfaces within and/or at the top of the reef.

## Introduction to reflection seismology

Reflection seismology provides a large-scale, low-resolution view of geologic structures compared to the details of outcrop or modern sediment. Reflection seismology refers to the records of man-made elastic waves that travel in the subsurface and get reflected or refracted at rock body boundaries (Sheriff and Geldart, 1995). Rock properties governing the behavior of these waves are rock sonic velocity,  $V$ , and density,  $\rho$ . Sedimentary rocks are particularly well suited to seismic imaging, because, in general,  $V$  and  $\rho$  change gradually along bedding, but abruptly across bedding planes. Incident waves are split into a reflected part that travels upward, and a refracted part that continues downward in a different direction, and can be reflected at a deeper bed boundary. Multiple layers are imaged by the seismic tool, and the amplitude of the reflected waves is the reflection coefficient, RC. It is given by

$$\text{RC} = (\rho_2 V_2 - \rho_1 V_1) / (\rho_2 V_2 + \rho_1 V_1)$$

The products  $\rho V$  represent the acoustic impedance of the layers 1 (upper) and 2 (lower) respectively. Seismic surveys proceed by collecting data at closely spaced intervals

along surface profiles. The vertical seismic record is travel time, and must be converted to depth. This requires measuring velocity and density in boreholes, and correcting seismic velocities measured by the survey. In addition, horizontal reflectors will record reflections vertically below shot points, but dipping reflectors, abrupt terminations of reflectors, and reflections that originate out of the plane of the survey line (“side echoes”) must be corrected by “migration” of the reflections in the time domain (Figure 1). Correcting for dipping reflectors and abrupt reflector terminations is particularly important in imaging reefs, where fore-slopes can be steep (up to  $90^\circ$ ), and lateral facies changes can be abrupt (e.g., thin-to-thick bedded back reef sediments to massive bedded reef margin sediments).

Seismic resolution is of critical importance in imaging reefs. Generally, two reflectors can be recognized or resolved as separate events, if the distance between them is at least  $\frac{1}{4}$  wavelength. Wavelength,  $\lambda$ , is given by

$$\lambda = V/f$$

Where  $V$  is the sonic velocity and  $f$  is the frequency. Higher resolution results from a broad bandwidth of frequency. High-frequency waves are attenuated faster than low-frequency waves, and the frequency content will decrease with depth.

Seismic imaging is also affected by the type of survey that is collected. Two-dimensional (2D) seismic surveys are comprised of widely spaced profiles, generally greater than or equal to 1 km in spacing, and are more difficult to correct for dipping reflectors and side echoes, diminishing resolution. Three-dimensional (3D) seismic surveys have closely spaced shot and receiver positions (commonly  $\leq 25$ – $50$  m), and are more successfully migrated, increasing data quality and resolution. This has significantly improved the seismic imaging of seismic reefs (Masaffer et al., 2004).

## Rock properties, geophysical response, and the challenges of carbonate imaging

Carbonate rocks possess rock properties and geometries that present imaging challenges (Taner, 1997; Sarg and Schuelke, 2003).

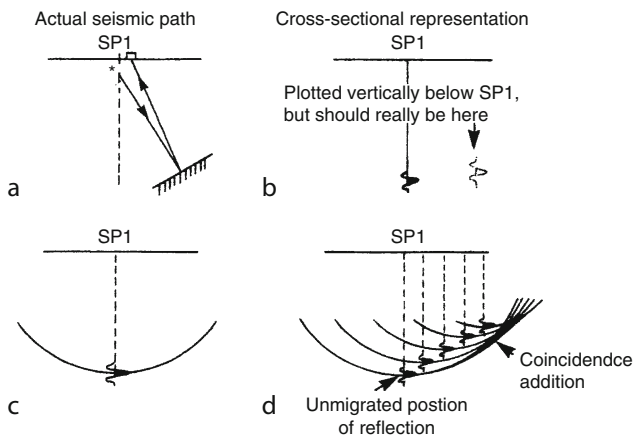
1. For carbonate rocks  $V$  is large, often ranging from 4,500 to 6,000 m/s, and  $f$  is low because of high attenuation in massively bedded rocks with heterogeneous pore structures. These characteristics result in long wavelengths, and relatively low seismic resolution in reefs.
2. Velocity appears more controlled by the combined effects of depositional lithology, and diagenetic processes, like cementation and dissolution (Anselmetti and Eberli, 1997). The ranges within  $V_p$  and  $V_s$  are caused mainly by variations in amount of porosity and porosity type, and not by variations in mineralogy. Velocities show a positive correlation with density and an inverse correlation with porosity, but departures can



be significant. Rocks with moldic or intraframe porosity are dominated by matrix velocity and have higher velocities, whereas rocks with pervasive interparticle, intercrystalline, or microporosity have relatively lower velocities (Anselmetti and Eberli, 1997).

3. High-velocity carbonate layers also cause high-velocity heterogeneity and velocity anisotropy. As the incidence angle increases, the corresponding average travel velocity increases. Consequently, velocity increases with increasing offset of shot points to receiver points.
4. Carbonate platforms can have steeply dipping foreslopes that provide imaging challenges similar to those that occur with steeply dipping faults (e.g., dispersion and diffraction).

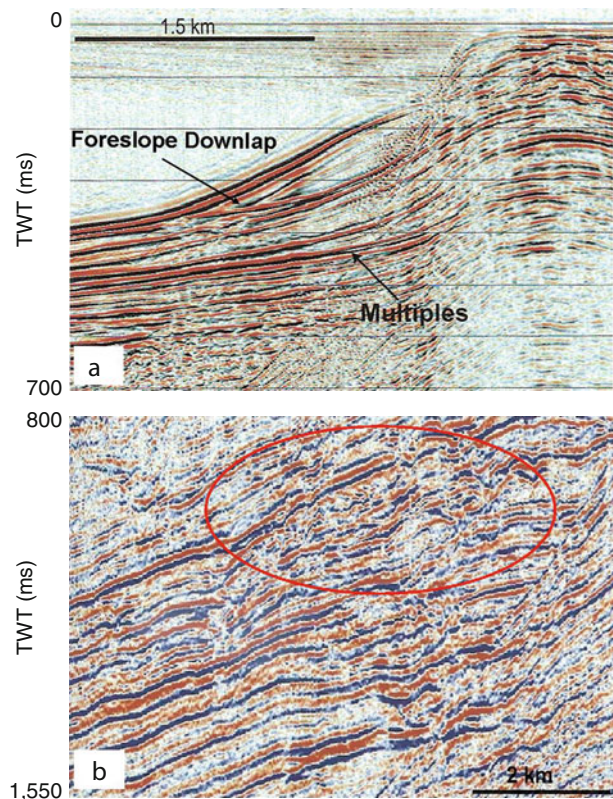
The complexity of bed and pore geometry within carbonate platform successions thus has a major effect on the geophysical response of carbonates (Sarg and Schuelke, 2003; Schlager, 2005). Platform margin reef facies are often massive bedded units with a complex amalgamation of mounded, and flat and dipping planar beds. This results in both horizontal and vertical anisotropy at the scale of one to tens or hundreds of meters. A mounded, chaotic seismic facies is common for reefs. Extensive karst formation can disrupt the normal bedding patterns making for chaotic stratal patterns, and dissolution expanded and enhanced fractures. This provides opportunity for complex ray paths, dispersion of wave fronts, and multiple diffraction points. Although often causing a distinctive chaotic seismic facies, with circular sinkhole and collapse features, resolution in this kind of terrain is generally lowered.



**Seismic Reflection, Figure 1** Seismic migration. Unmigrated reflections are plotted vertically below the shot point (b). This is correct for horizontal reflectors, but not for the dipping reflector shown in (a). Correction is done by migration, illustrated in (c) and (d). (c) shows all the possible sources that might have produced the reflection observed at shot point 1 (SP1), lying on a semicircle around SP1. (d) shows this process repeated for subsequent shot points, where the semicircles coincide in a zone on the right. This zone of coincident circles approximates the true position of the reflector (from Schlager, 2005).

## Reef architecture

The term reef denotes a wave-resistant buildup formed by the interplay of organic frame building, erosion, sedimentation, and cementation (Wright and Burchette, 1996). The basic controls on reef geometry are upward growth of the organic framework, current reinforcement by this structure, and sediment export by the reef factory. Reefs generally shed sediment of a wide range of sizes, and this material forms debris aprons that thin away from the reef core. Dunham (1970) distinguished between ecologic reefs, built and bound by organisms, and stratigraphic reefs where the binding may also be done by cementation of loose sediment. “Seismic reefs” defined by geometry and reflection character include either type. The seismic tool images reefs where many generations



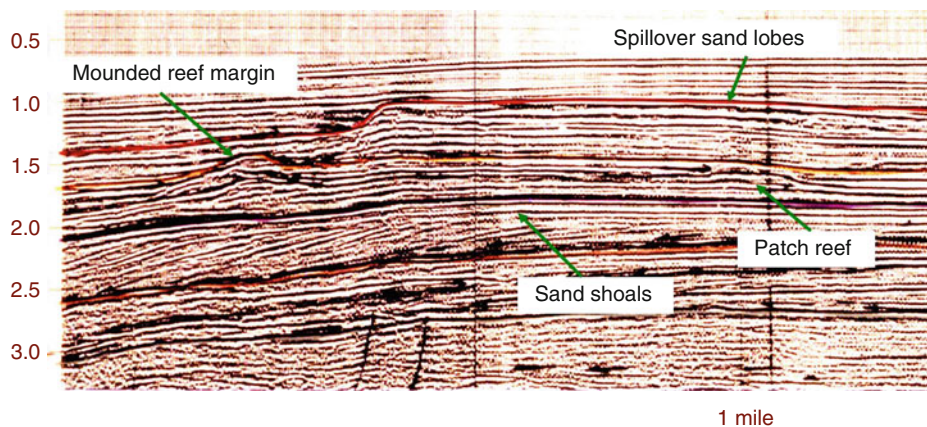
**Seismic Reflection, Figure 2** 2D seismic. (a) Two-dimensional (2D) seismic image of the margin of western Bahama Bank. Modern margin with characteristic near-vertical wall, and cemented upper slope, overlapped by transparent facies of unconsolidated Holocene slope deposits. Steeply dipping diffractions help define the reef margin. Also present in lower right center of figure are a train of multiples generated from the hard interface between the Holocene sediments and the well-cemented Pleistocene slope deposits. Convergent fore-slope beds of Pleistocene periplatform and planktonic material occur seaward of the reef margin (modified after Eberli et al., 2004a). (b) Western Great Bahama Bank middle to lower slope showing discontinuous reflections on a channelized slope (within oval) (from Eberli et al., 2004a).

of reef growth were stacked to thicknesses of tens to hundreds of meters. Sand shoals that interfinger with reefs may also be included in the seismic reef unit.

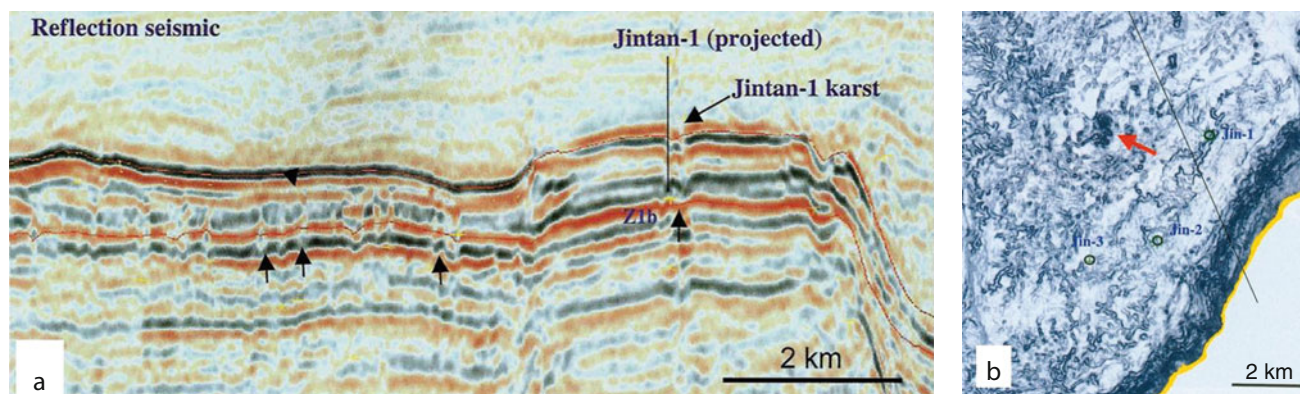
### Reef seismic facies

Seismic reefs can be divided into a number of seismic facies (Figures 2, 3, and 4) (Sarg, 1988). The reef margin lithofacies is comprised of wave-resistant barrier reefs rimming the platform or belts of knoll and skeletal sands, and in many places, it has the most distinct seismic facies. Reef margins are heterogeneous, massively bedded

features, and image most commonly as mounded, chaotic seismic facies (Figures 2 and 3). Reef margins generally show abrupt lateral facies transitions to both platform interior, and fore-slope seismic facies. Platform interior lithofacies can range from near-reef sand aprons grading shelfward into restricted to normal marine lagoons. Depending on the degree of restriction, lagoons are composed of mixed muddy, sandy, and patch reef subfacies. The relative proportion of these subfacies is dependent on the grain size of local sediment production, and the efficiency of winnowing by waves and tidal currents.



**Seismic Reflection, Figure 3** NW Shelf Australia. Two-dimensional seismic of Tertiary carbonates off the northwest shelf of Australia, displaying a range of seismic facies across a broad passive margin shelf. Mounded, gently prograding, stacked buildups define the Miocene reef margin, and shelfward (to right) patch reefs or small isolated reef platforms occur within parallel bedded platform interior reflections. An older Paleocene-aged prograding bank displays oblique prograding geometry, where horizontal reflections define banktop bioclastic shoals, and dipping clinothems are composed of calcareous marls. The Pliocene section, overlying the mounded Miocene, is characterized by an eroded and truncated margin, and reflections dipping into the platform interior, and composed of bioclastic spillover sand lobes.



**Seismic Reflection, Figure 4** Seismic karst (a) Three-dimensional (3D) seismic reflection section of Jintan buildup (Miocene), Luconia Province, Malaysia. Interruptions of the reflections (arrows) are interpreted to represent a combination of fracturing and karst sinkholes. Most karst is associated with the top Zone Zb1, but some features reach to the top of the carbonate in the center of the Jintan buildup (from Vahrenkamp et al., 2004). (b) Horizon coherence or discontinuity time slice, 32 ms below the Zb1 unconformity. Discontinuities are made explicit by filtering the seismic to highlight discontinuities or areas where adjacent seismic events are different or discontinuous. In this time slice, sinkholes and other solution features are displayed as small circular to tubular features. The dark blotch (red arrow) is interpreted to represent a collapsed cave (from Vahrenkamp et al., 2004).



Seismically, the platform interior is characterized by parallel reflections of varying amplitude, where impedance contrasts are defined by porosity changes at bed boundaries (Figures 2 and 3). The seaward facing fore-slope lithofacies is a distinctly inclined unit, commonly displaying from 4° to 5° to near-vertical dips. Sediment is predominantly reworked platform material with pelagic admixtures, and has highly variable grain size from gentle muddy slopes to sandy or rubbly slopes with steep, planar foresets (Kenter, 1990). Seismically, the fore-slope is characterized by sigmoid to oblique clinoforms (Figures 2 and 3). Where channels dissect the slope, seismic facies are characterized by discontinuous reflectivity (Figure 2b). The toe-of-slope apron and basin lithofacies are moderately inclined ( $\geq 1.5^\circ$ ) to flat seafloors seaward of the fore-slope (Figure 3). Grain size is variable, ranging from well-defined graded beds, to fine-grained breccias, and muddy sediment, containing redeposited benthic and planktonic biota. Seismic facies are commonly convergent to parallel reflections of variable amplitude that may show downlapping terminations (Figures 2a and 3).

### Seismic expression of karst

Repeated exposure to fresh water results in solution and karst landscapes in humid carbonate terrains. These karst landscapes exhibit positive relief features like tower, or pinnacle karst that can be up to 300 m in relief, and negative dissolution features, such as sinkholes, caves, and karst collapse. The irregular shape and distribution of these features reflect seismic waves in a chaotic manner, which makes them hard to image in 2D seismic data. On 2D data, subaerial exposure and negative karst features often need to be inferred from their association with unconformities and erosional truncation, or the presence of chaotic seismic facies (Eberli et al., 2004b). Three-dimensional seismic data has largely overcome the problem of diffracted and dispersed seismic waves in karst terrains (Heubeck et al., 2004; Isern et al., 2004; Vahrenkamp et al., 2004). The concave-up sinkhole reflections of Figure 4 or irregular hummocky reflection patterns directly indicate negative karst features.

### Summary

Seismic imaging of carbonate platforms and coral reefs has markedly improved with the advent of modern 2D and 3D seismic data. Reflection seismic imaging does present challenges because of the unique characteristics of reefs, including high velocities, abrupt lateral facies changes, and steeply dipping fore-slope deposits. These result in lowered resolution, and diffractions and dispersion of elastic seismic waves that degrade the seismic images. Characteristic seismic facies include (1) mounded to chaotic seismic of reef margin and reef core lithofacies; (2) parallel, concordant reflectivity in back-reef and platform interior settings; (3) sigmoid to oblique prograding seismic facies in fore-slope environments, and (4) convergent to parallel reflection character in the toe-of-slope to

basin settings. Karst dissolution is expressed as concave upward and chaotic seismic facies in sinkhole and karst collapse terrains, and as positive relief, tower, and pinnacle features.

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## Cross-references

[Bioherms and Biostromes](#)  
[Last Glacial Lowstand and Shelf Exposure](#)  
[Reef Structure](#)  
[Remote Sensing](#)  
[Seismic Refraction](#)

## SEISMIC REFRACTION

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### Definition

*Seismic refraction.* Geophysical research method used to map the subsurface and internal structure of modern coral reefs.

### Introduction

Geophysical research methods such as seismic refraction and seismic reflection (see [Seismic Reflection](#)) techniques have been used to map the subsurface and internal structure of modern coral reefs. These methods rely upon the refraction or reflection of a seismic pulse (also referred to as a sonic, acoustic, or elastic pulse) at a seismic discontinuity, where there is a physical property contrast in the density and elasticity of the contiguous materials. In a geological context, the contrast may represent changes in mineralogy, lithology, porosity, cementation, diagenesis, or lithostatic pressure.

Seismic methods can thus be used to map subsurface discontinuities and determine thicknesses of strata allowing stratigraphic inferences to be made. Continuous seismic reflection (see [Seismic Reflection](#)) surveys can provide good inter-reefal data and in some cases, such as Purdy's study of the Belize reefs (Purdy, 1974), reveal the internal reef structure of modern reefs. However, the attenuation of the signal in continuous seismic reflection surveys is usually affected by steep reef surfaces so that sub-bottom reflectors become no longer detectable. In these cases, seismic refraction techniques are more useful.

In 1946, 1950, and 1952, seismic refraction programs were conducted on Pacific atolls, and data were obtained on the deep structure beneath Bikini, Kwajalein, and Eniwetak atolls (Dobrin and Perkins, 1954; Raitt, 1954, 1957). Near-surface seismic refraction investigations were also carried out in 1971 and 1972 at Eniwetak atoll, where at least two solution unconformities were identified (Henny et al., 1974) indicating the utility of the seismic refraction method for shallow subsurface investigations of reefs.

### Method

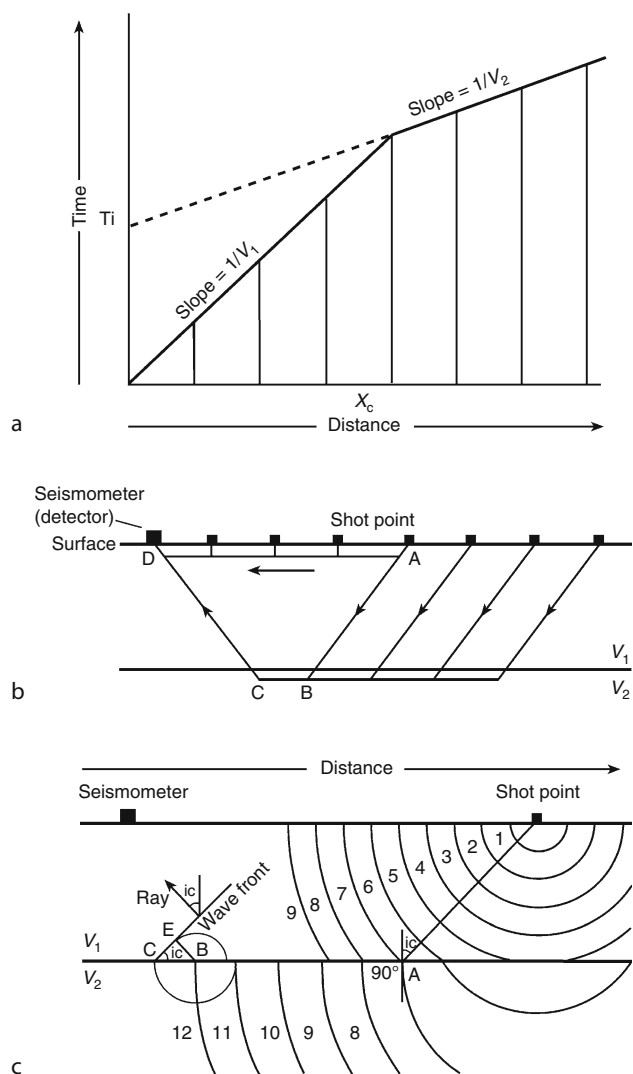
The seismic refraction method requires an increase in seismic velocity with depth across the refracting interface. The method involves the measurement of the time between the initiation of a seismic pulse at the shot point and its first arrival at the seismometer (detector), which is a measured distance from the shot point. These first arrivals (compressional refraction or p-waves) are usually the only ones considered in seismic refraction, although it is possible to use second arrivals (Dobrin, 1976). Arrival times for these waves are measured for incremental shot point/detector separations and plotted on a time distance graph as shown in [Figure 1a](#).

The seismic pulse for small studies using portable seismographs is usually generated at the shot point by either a hammer blow to a steel plate (to provide maximum coupling with the surface) or by the use of a small explosion. For a single-channel seismograph, the shot point is usually moved progressively away from the seismometer ([Figure 1b](#)), but with multichannel equipment, a larger shot is used in conjunction with a seismometer array.

The paths of the refracted waves, in a simple parallel two-layer case, travel in a straight line through a constant velocity medium  $V_1$  and are refracted along the boundary of the higher velocity layer  $V_2$  where there is a physical property contrast in the density and elasticity of the contiguous layers ([Figure 1b](#)). The angle of refraction ( $r$ ) is given by Snell's Law and is shown at point A on wavefront 7 in [Figure 1c](#) where the tangent to the sphere in the lower medium becomes perpendicular to the medium, and the ray travels along the boundary at the new speed  $V_2$  of the underlying strata. At a certain distance  $X_c$  ([Figure 1a](#)), the wave which has been refracted along the discontinuity will reach the surface at the same time as the one that has traveled the direct path in the lower velocity medium. At distances greater than this crossover time, the wave refracted along the surface of the discontinuity will reach the seismometer first and will therefore be represented on the seismic record as the first arrival. It is these first arrival or compressional refraction waves that are mostly used in refraction studies. There are different techniques for interpreting these seismic data.

### Reef studies using seismic refraction

Apart from the early use of deep seismic refraction in the 1940s and 1950s on the Pacific atolls, the use of shallow seismic refraction techniques for detailed modern reef studies is not apparent from the literature until the 1970s when such studies were conducted on Eniwetak atoll in the Pacific, using a 12-channel portable seismograph (Henny et al., 1974) and on the Great Barrier Reef of Australia using a single-channel portable seismograph (Harvey, 1977a, 1977b, 1986; Harvey et al., 1979; Harvey and Searle, 1983; Searle and Harvey, 1982; Searle et al., 1982). The use and adaptation of single-channel seismic refraction techniques, as a methodology for studying



**Seismic Refraction, Figure 1** (a) Arrival times for compressional refraction or p-waves are measured for incremental shot point/detector separations and plotted on a time–distance graph. (b) For a single-channel seismograph, the shot point is usually moved progressively away from the seismometer, but with multichannel equipment, a larger shot is used in conjunction with a seismometer array. The paths of the refracted waves, in a simple parallel two-layer case, travel in a straight line through a constant velocity medium  $V_1$  and are refracted along the boundary of the higher velocity layer  $V_2$  where there is a physical property contrast in the density and elasticity of the contiguous layers. (c) The angle of refraction ( $r$ ) is given by Snell's Law and is shown at point A on wavefront 7 where the tangent to the sphere in the lower medium becomes perpendicular to the boundary at the new speed  $V_2$  of the underlying strata.

reef-top structure is discussed by Harvey (1977a). The technique utilized across exposed reef surfaces employed a hammer and plate with an inertia trigger as a signal source and a geophone receiver. A major challenge was the insulation of electrical equipment in the marine

environment and also the adaptation of conventional steel plates to provide an elevated point of hammer contact when working in shallow reef pools. The technique was also used in shallow lagoon environments where transects were laid out using float lines and small dinghies. Although time consuming, it did allow seismic survey among closely spaced coral colonies where continuous recording hydrosondes could not be used. In this case, seismic detonators were used as a signal source and a hydrophone as a receiver (Harvey, 1977a).

These techniques were used to identify a refracting surface at three separate sites on the Great Barrier Reef where pre-Holocene sediments had previously been identified from borehole data. The seismic refractor at each of these sites was then correlated with a pre-Holocene substrate beneath the modern reef (Harvey et al., 1979).

Shallow seismic refraction studies were conducted on 30 individual reefs from Bewick Island ( $14^{\circ}26'S$ ) in the northern Great Barrier Reef to Lady Musgrave Reef ( $23^{\circ}24'S$ ) in the southern Great Barrier Reef with varying lengths of seismic profiling conducted for each reef (Harvey, 1977b, 1986). The combined seismic results from all 30 reefs show that the depth of the refractor varies from 3.9 to 24 m below the modern reef surface. This refractor on average is highest below the modern reef rim and lowest below the modern reef lagoons demonstrating that the relief on the older pre-Holocene substrate is correlated with the relief of the modern reef surface (Harvey 1986). At the start of the seismic refraction study program, there were only three reefs in the Great Barrier Reef where the pre-Holocene substrate had been identified in borehole data so that the refraction data were relied upon to identify the equivalent surface on the other 27 reefs. Subsequently, borehole data have been acquired for about half of these reefs and have verified the location of the pre-Holocene substrate (Harvey, 1986).

Searle and Harvey (1982) combine the use of inter-reefal continuous seismic profiling with reef-top shallow seismic refraction data across Michaelmas reef (Lat  $16^{\circ}35'S$ ) to demonstrate how the reef-top refracting surface is correlated with a strong seismic reflector on either side of the reef. This shallowest and most prominent sub-bottom reflector has been interpreted as the Holocene/pre-Holocene sedimentary boundary (see *Seismic Reflection*). However, this reflector is not detectable close to the reef-top surface because of attenuation of the reflection data. Thus, the refraction method is more useful in providing subsurface data on the reef-top itself and these data can be used together with the reflection data to provide a more complete record of the extent of the pre-Holocene substrate.

Searle et al. (1982) and Harvey and Searle (1983) discuss the interpretation of shallow seismic data for the Great Barrier Reef for both reefal and inter-reefal areas and demonstrate how seismic refraction and seismic reflection data can provide complementary data in order to obtain a better picture of the nature and extent of the pre-Holocene surface in the Great Barrier Reef region.

Seismic refraction data are also used in reef evolution studies to supplement geological data or to fill gaps in the data. For example, Johnson and Searle (1984) use refraction data in their identification of postglacial stratigraphy in the central Great Barrier Reef and Rees et al. (2006) use refraction data in their analysis of the Holocene granite-based reef systems in the northern Great Barrier Reef. These demonstrate the utility of the seismic refraction studies on reef-top surfaces, particularly where geological data do not exist.

## Summary

Seismic refraction is a geophysical research method that uses a refracted seismic pulse to map the subsurface and internal structure of modern coral reefs. Seismic refraction techniques are more useful than seismic reflection techniques in cases where the attenuation of the signal in continuous seismic reflection surveys is affected by steep reef surfaces so that sub-bottom reflectors become no longer detectable. However, Searle et al. (1982) and Harvey and Searle (1983) demonstrate how seismic refraction and seismic reflection techniques can provide complementary data in reef investigations.

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## Cross-references

[Seismic Reflection](#)  
[Solution Unconformities](#)

## SHINGLE RIDGES

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## Definition

Coral shingle ridges are convex up/top accumulations of coral fragments, often broken from near-shore reefs and deposited landward of the high tide level by storm waves. Over centuries to millennia, successive storms deposit a number of ridges that lie parallel or sub-parallel to the shore.

## Introduction

Coral shingle ridges often occur in locations where coral reefs occur close to shore. They are deposits of coral fragments forming a ridge that lies parallel or sub-parallel to the coast. These ridges can be up to 6 m high above the mean sea level, several tens of meters wide and can extend along the shore for hundreds of meters. Eye witness reports of their emplacement reveal that they are deposited during intense storms (often tropical cyclones) when coral fragments are eroded from near-shore reefs by wave action (Hughes, 1999; Davies, 1983; Baines et al., 1974; Rasser and Riegl, 2002; Nott, 2003). These ridges form a record of past tropical cyclones and/or intense storms and can be used to determine the frequency and magnitude of these events of many millennia. As such they can provide a valuable insight into the long-term behavior of storms over a region and help to elucidate the natural variability of the events from anthropogenic influences.

## Formation of coral shingle ridges

The source of the coral fragments deposited in the ridges can either come from living corals or it can also be transported from existing accumulations of coral shingle in the offshore zone. These offshore accumulations result from a number of erosional processes such as biodegradation and wave action during both storms and fair weather



conditions (Rasser and Riegl, 2002; Hughes, 1999). It is thought that the angle of the offshore reef slope plays a role in whether the eroded fragments are transported predominantly offshore or onshore. Steep reef fore-slopes, favor offshore transport of fragments, often to depths of greater than 50 m which is too deep to be reworked and transported by storm waves. Shallow sloping, and particularly wide reef fronts favor transport onshore and the formation of coral shingle ridges. However, some sites, such as Curacoa Island in the central Great Barrier Reef, Australia that are fronted by narrow, steep reef slopes have extensive coral shingle ridge development on land (Hayne and Chappell, 2001; Nott and Hayne, 2001). These sites with presumably minimal accumulation of coral shingle in the shallow waters of the reef and maximum accumulation of shingle in the deeper offshore waters below the wave base (depth to which waves will entrain and transport sediment on ocean floor), suggest that the onshore ridges could have formed from predominantly live coral fragments broken off during the storm. At other sites, however, there can be little doubt that onshore ridges were formed from the reworking of existing accumulations of shingle in the shallow waters offshore.

It is difficult to know whether the shingle ridge is deposited gradually during the storm, or as one, or a series of, sediment units moving landward from existing offshore accumulations. Scoffin (1993) has described coral shingle ridge building as ridges that

have been transported and deposited like large asymmetric waves of sediment; material picked up on the seaward side is rolled up the ridge and dropped down the advancing slope

suggesting, that an entire, or substantial part of an offshore accumulation of shingle is moved onshore as a single unit during the storm. If on the other hand, ridges accumulate gradually, then the ridge could be assumed to increase in height over a period of time during the storm. In this instance wave run-up (the uprush of waves against or over an object or sloping shoreline, respectively) may play a role in their formation.

It is likely that the height of an onshore coral shingle ridge is a function of the mean storm, still water level being the storm surge, tide and wave set-up (addition to the water level from broken waves) combined, and possibly wave run-up. Ascertaining to what extent wave run-up is responsible for the height of the resulting ridge is important, as run-up can equal or exceed the height of the storm surge depending upon various conditions. Wave run-up is a function of significant wave height ( $H_s$ ) and wave period/length, wave refraction/diffraction, bathymetry, beach slope angle, and roughness and permeability of beach material (Nielsen and Hanslow, 1991). With very rough, coarse-grained, permeable substrates Losada and Gimenez-Curto (1981) note wave run-up can be 0.30–0.75 times that of run-up on a sandy, largely impermeable beach under the same storm conditions. Observations of historical storm surge emplaced coral shingle ridges suggest that wave run-up may play an insignificant role. For

example, a 3.5-m-high ridge was deposited on Funafuti Atoll during Tropical Cyclone Bebe in 1971. The surge accompanying the storm was 5 m above the level of the reef flat, or mean low tide level, and 1.5 m higher than the elevation of the resulting ridge crest (Maragos et al., 1973). A similar situation occurred at Mission Beach, south of Cairns, North Queensland in Australia, where an intense tropical cyclone struck in March 1918. Here, a 4.5–5.1-m-high ridge of pumice was deposited by a surge as the tropical cyclone crossed the coast. Eyewitness observations and results from numerical storm surge and wave models of the event, along with knowledge of the tide level at the time, show that the storm tide (surge plus tide) and wave set-up combined, amounted to an inundation level of 4.7–4.9 m (Nott, 2003). This suggests that wave run-up could have only contributed 0.2–0.4 m of the ridge height at its highest elevation. Elsewhere, where the ridge is only 4.5 m high, the wave run-up does not appear to have contributed to the formation of the pumice ridge. It would appear therefore, that in at least some instances the height of the crest of coral shingle and pumice ridges is close to or less than the height of the storm tide and wave set-up combined. This does not mean, however, that progressive accumulation or accretion of a ridge cannot occur during the storm. But it does mean that wave run-up may not always be an important process in ridge accretion.

### Sedimentary and stratigraphic characteristics and preservation potential

Coral shingle ridges contain a number of distinct sedimentary facies or units of sediment. These include storm beach face, berm, crest and washover facies (Hayne and Chappell, 2001). Beach face and berm facies include porous, clast supported, coarse biogenic shingle deposits that occasionally dip seawards but are usually structureless. Crest facies are horizontally bedded and are finer-grained than beach face deposits. Washover facies are bedded, dip landward up to 15° and sometimes contain imbricated clasts (imbrication is a sedimentary feature where particles are arranged in an overlapping shingle-like pattern dipping in one direction). Each of these facies or units combines to make a storm deposit. Storm deposits are often separated by groundsurfaces being lenses of pumice pebbles and a weak sooty or earthy palaeosol (ancient soil). These groundsurfaces are really former groundsurfaces, or the surface of the feature that was exposed for a sufficient period of time between individual tropical cyclone events so that some soil development was able to take place. Ridges often contain only one storm deposit, but it is possible for two or more storm deposits to occur in one ridge. Careful excavation of the ridge is necessary in order to determine the number of storm deposits making up the ridge. Samples collected for geological dating from only one storm deposit, when more than one storm deposit is present, may bias the age determination of that ridge.

Coral shingle ridges often accumulate on the sheltered side of islands, presumably because on the exposed sides they are constantly removed by the largest or the most intense tropical cyclones affecting a region. The sheltered sides will experience diminished wave energy, but will still experience the full effects of the surge. As the wave energy is reduced, the likelihood of the ridge being removed during subsequent cyclones is lessened. Where, the preservation potential for ridges is high, such as on the lee side of islands, a number of ridges are sometimes able to accumulate over a period of time. Curacao Island on the Great Barrier Reef has 22 consecutive coral shingle ridges parallel to the shore on its northwestern or sheltered side. Individual ridges extend for over 100 m along the shore and rise to over 5 m above the mid-tide level (the tidal range here is approximately 3 m). The ridges were deposited by successive tropical cyclones so that new ridges are deposited seaward of the previously emplaced ridge. The age of the ridges increases progressively with distance, inland (Hayne and Chappell, 2001; Nott and Hayne, 2001). Curacao Island is typical of many sites that preserve coral shingle ridges; however, not all sites retain as many ridges. Elsewhere, only one or two ridges paralleling the shore are preserved. This is often due to the site exposure and the frequency of cyclones in the region. The time interval between cyclones will determine the extent to which compaction and lithification or induration of the ridge can proceed. Over a period of time, individual coral clasts within a ridge begin to weather or break down, and in so doing provide carbonate that will progressively cement clasts together. Cementation usually begins within the core of the ridge, and it is common for loose fragments to remain on the crest and sides of the ridge several centuries after deposition. The ridge becomes progressively resistant to further wave attack over time. However, looser fragments on the ridge crest can be removed and replaced by younger fragments if subsequent storm surges are sufficiently high to be able to overtop that ridge. In this fashion also, more recent storm deposits can be superimposed on older ones. Prior to stabilization, and depending upon the geomorphic setting, ridges can move inland by waves washing over the ridges and transporting clasts to the landward side of the ridge. The 19-km-long, 3.5-m-high and 35-m-wide coral shingle ridge deposited by Tropical Cyclone Bebe on Funafuti Atoll continued to move inland and along the shore for many years (Baines and McLean, 1976). Indeed, in some instances on coral atolls, the ridges will move across the reef flat and abut or lap onto existing ridges through normal, non-cyclonic, wave action. Individual storm or cyclone deposits and ridges will be more difficult to recognize at these locations compared to sites such as Curacao Island where individual ridges often remain separated from each other.

### Shingle ridges as records of the frequency and intensity of tropical cyclones

Coral shingle ridges can provide valuable data on the frequency and intensity of the tropical cyclones responsible

for their emplacement (Chappell et al., 1983; Chivas et al., 1986; Hayne and Chappell, 2001; Nott and Hayne, 2001; Nott, 2003). By dating most, if not all, of the ridges at a site, the total number of ridge building tropical cyclones over a period of time can be ascertained. Of course, the rate of ridge building is dependent upon the number of tropical cyclones passing the area with time and also the rate of coral reef replenishment or regeneration. Hayne and Chappell (2001) concluded that the narrow, fringing coral reef, which was the source of shingle for the ridges on Curacao Island, was able to regenerate after 80 years which was well below the apparent recurrence interval of ridge building (storm deposit) events of 280 years. The other ridge sites along the length of the Great Barrier Reef showed that ridge building events have occurred on an average every 177–280 years (Nott and Hayne, 2001). Furthermore all of these studies (Chappell et al., 1983; Chivas et al., 1986; Hayne and Chappell, 2001; Nott and Hayne, 2001; Nott, 2003) concluded that tropical cyclone frequencies have remained unchanged in the northeast Australian (Coral Sea) region over the last 3,000–5,000 years.

A method to determine the intensity of the prehistoric tropical cyclones responsible for building ridges was introduced by Nott and Hayne (2001) and Nott (2003). The height of these ridges was assumed to represent the minimum height of the storm inundation during the event responsible. The elevation of these features was accurately surveyed to datum, and samples of coral and/or shell radiocarbon dated to determine the minimum height and times of inundation, respectively. The height of this inundation was then related to the intensity of the palaeocyclone, which is determined through the use of numerical storm surge and shallow water wave models. The models are used to determine the relationship between surge height and central pressure for each shingle ridge location. In addition, the relationship between surge height and translational velocity of the cyclone, the radius of maximum winds and the track angle of the cyclone as it approaches and crosses the coast are determined. Model results are compared to the measured surge heights from recent or historical cyclone events near the study sites. The central pressure of the cyclone responsible for the formation of the ridge is then determined by modeling the magnitude of the surge plus wave set-up, wave run-up and tide required to inundate the ridge.

Nott and Hayne (2001) found that the coral shingle ridge sequences along the Great Barrier Reef were primarily recording only the largest or most intense tropical cyclones, and were not registering the smaller less intense events over a period of time. The ridge building events were very intense category 4 and category 5 tropical cyclones and they have had an average return interval of between 200 and 300 years over the past 5,000 years (Nott and Hayne, 2001).

The possible caveats to the technique for determining the magnitude of prehistoric tropical cyclones are the lack of inclusion of the influence of hydroisostasy on

the present day elevation of the prehistoric cyclone deposits, and the imprecision in calculating the wave run-up during the prehistoric event. Nott and Hayne (2001) and Nott (2003) recognize these possible caveats, and note that sea levels have fallen, due to hydroisostasy, over the period of the prehistoric record. However, if this is taken into account in the analysis of the intensity of the prehistoric storms, the older deposits (coral shingle ridges deposited between 3,000 and 5,500 years BP) should be higher in elevation than the younger more shoreward ridges. Topographic surveying of the ridges shows that this is often not the case. The coral shingle ridges compact over a period of time, and there is evidence also to suggest that the ridge crests have been overtopped by storm surge and waves, further reducing their height since deposition. Nott and Hayne (2001) suggested that this reduction in elevation of ridge crests would likely more than compensate for the effects of sea-level fall since termination of the Holocene transgression. In addition, if sea-level fall was taken into account it would suggest that the ridges deposited since approximately 2,500–3,000 years BP, or since sea levels stabilized close to their present height, would have been deposited by more intense cyclones. Such an interpretation would suggest that these storms were becoming more intense with time. Independent studies of other ridge sequences (sand and shell ridges) throughout the region and also studies using isotopic signatures of tropical cyclones in limestone stalagmites suggest that there has not been a substantial increase in the intensity of tropical cyclones in this region to the present day (Nott, 2006; Nott et al., 2007).

## Summary

Coral shingle ridges form where coral reefs lie close to shore. Waves during intense storms or tropical cyclones break fragile coral species into fragments that can accumulate as a (shingle) deposit landward of the high tide mark or as an offshore deposit that may or may not be transported landward at a later date. The onshore deposits of coral shingle are shaped into a ridge by the marine inundation constituting a storm surge, tide, wave set-up, wave action and wave run-up. Successive ridges are deposited with time so that multiple shore parallel ridges can eventually form into a ridge plain. Each new ridge is deposited seaward of the previous ridge and often, but not always, one ridge can be deposited during a single tropical cyclone event.

The ridge plains can provide a valuable record of the frequency and intensity of tropical cyclones for that region over several millennia. Recent examination of several ridge plains along the Great Barrier Reef region show that these ridges are often emplaced during intense tropical cyclones and these events occur on an average every two to three centuries. This is an order of magnitude greater than that suggested by the short historical record of these events in this region.

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## SOILS OF LOW ELEVATION CORAL STRUCTURES

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## Definition and introduction

Low elevation coral structures include atolls (essentially reefs of variable thickness built up by corals (and other organisms) resting on a volcanic base) and reef platforms having an elevation generally less than 5 m above mean sea level. They are unique to tropical and certain subtropical oceans since the reef-building organisms require water temperatures in excess of 22°C. These features are



widespread in the central and south Pacific, the central Indian Ocean, and parts of the Caribbean (Lesser Antilles and Bahamas), with a few examples in the Atlantic Ocean. Some countries consist entirely of low elevation coral structures, e.g., Kiribati, Maldives; others contain atoll groups, e.g., the outer Islands of the Seychelles; and some countries consist of mainly volcanic islands with a few isolated atolls, e.g., Ontong Java in the Solomon Islands.

Cumberland (1956) has identified six types of island (in the Pacific) partly or wholly associated with coral reefs, but in this chapter focus will be on more or less continuous emerged or slightly emerged calcareous reefs, with minimal comment on any non-calcareous structures present. The main structures will be low atolls (reefs surrounding a lagoon) where the maximum height of the emerged portion (usually less than 5 m) is made up of accumulations of broken reef material deposited by storms, or emerged coral platforms with no associated lagoon. Low-lying fringing reefs occur around many tropical islands, but these will not be considered here.

The widely varied nature of low elevation coral structures makes generalization difficult, but many have some features in common. They usually have limited land area and few natural resources. Such islands, particularly in the eastern Pacific, have limited supplies of fresh water and many are subject to prolonged droughts. The groundwater is often brackish (slightly salty). This peculiar environment has resulted in the development of a specialized flora – a plant community adapted to saline, alkaline soils, subject to water stress and salt spray. The natural vegetation is mostly strand species recruited from the Indo-Pacific or similar strand flora of the shores of islands of all kinds in the tropics. The agriculture is also rather specialized, often being restricted to coconuts, pandanus, breadfruit, and such root crops as *Colocasia* and *Cyrtosperma* grown in pits dug down to the groundwater table.

The properties of coral soils are, in general, dominated to a large extent by the calcareous nature of the parent material, whether or not this is mixed with volcanic materials. The soils tend to be shallow, alkaline, and coarse textured, having carbonatic mineralogy except where there have been relatively recent additions of volcanic material. The soils are generally of very low silica content. The fertility is highly dependent on the organic matter content. Organic matter can be high in undisturbed soils under natural vegetation, but can decrease dramatically as a result of inappropriate cultivation techniques, e.g., land clearance and weed control by fire.

As for all tropical soils, organic matter in coral soils performs an important role in the concentration and cycling of plant nutrients. In coral soils, however, a second role – that of moisture retention – is equally important. Since low coral structure soils are frequently sandy and excessively well drained, the moisture retention in the absence of organic matter is very low (see Morrison, 1990); the total amount of water retained often remains low, and plants are subject to water stress unless the rainfall is high and relatively constant or they can tap the freshwater lens.

## Soil forming factors on low elevation coral structures

Soil forming factors include climate, parent material, relief, hydrology, flora (and fauna), time, and humans, although these are not independent of each other. For low elevation coral structures, many of these factors are relatively constant, but some important distinguishing features occur. For example, the climate consists of two components – temperature and rainfall. The climate for the areas of interest is relatively constant with mean annual temperatures ranging from about 22 to 35°C, while the rainfall (as expressed in mean annual terms) can vary from about 700 to over 3,000 mm/yr. The impact of rainfall variations produces significant differences in the vegetation type and quantity, and this in turn leads to different amounts of organic matter being available for incorporation into soils. The result is that soils in similar geomorphological positions in “wet” and “dry” locations can be quite different (see Figure 1).

As noted above, the parent materials are dominated by calcareous solids derived from reef growth, with varying additions of ash, scoria, pumice, and guano. The materials are generally coarse-grained varying from accumulations of boulders and cobbles to materials dominated by sand with some silt material. Clay size materials are not abundant in these soils. Relief is not normally a key factor for low elevation coral soils, as the elevations are <10 m and slopes are usually very gentle.

Hydrology can be a significant factor, as the position of the groundwater table can influence soil properties, use, and management. In addition, the freshness of the groundwater may have an impact on the vegetation diversity and density and thus impact on organic matter availability for soil incorporation. As noted above, vegetation density and diversity are highly rainfall dependent, although the diversity is generally quite limited. The influence of fauna is limited with crabs digging burrows, pigs digging in soils, birds depositing guano, and some introduced species such as rats and goats damaging the vegetation. Time is also relatively constant for coral soils, as most low elevation structures have been formed in the last 5–7,000 years (Woodroffe, 2008). The influence of humans varies from place to place mainly by changing the vegetation from native species to coconut plantations or growing of other food crops.

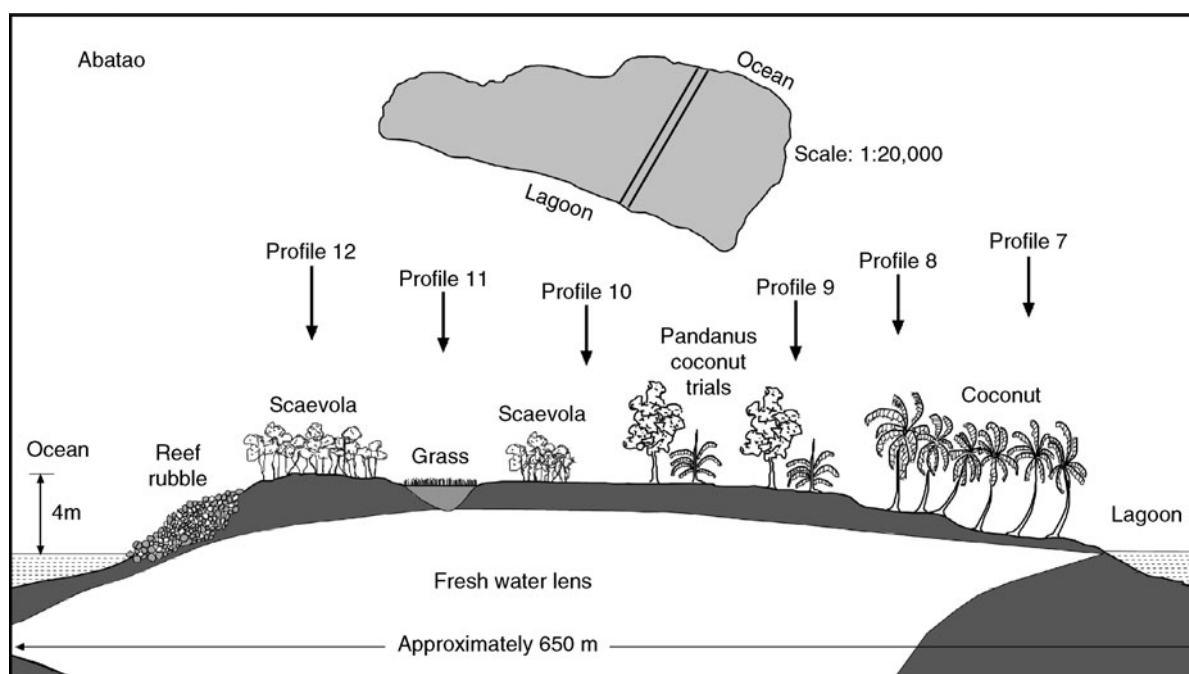
## Diversity of low elevation coral soils

Given the limited variation in the soil-forming factors outlined above, it might be considered surprising that there are many variations in coral soils; this is not, however, the case. As an example, the soils of the islet of Abatao in Tarawa, Kiribati, will be described (Morrison and Seru, 1986). The survey work relating to this islet was done in the 1980s, while most of the islet was the Kiribati Government Agricultural Research Station and minimal human urban impact had occurred (see Figure 2).

On moving from the Ocean to the Lagoon, a number of different profiles were observed. Close to the ocean side,



**Soils of Low Elevation Coral Structures, Figure 1** Comparison of soils in stable mid-island positions in different rainfall locations (a) Tarawa (wet) and (b) Kiritimati (dry).



**Soils of Low Elevation Coral Structures, Figure 2** Cross-section of the central part of Abatao Islet, Tawara, Kiribati (modified from Morrison and Seru, 1986; soil profiles are described in the text).

Profile 12 showed minimal profile development. There was a thin surface horizon showing some organic matter accumulation, but little or no structure. This surficial layer overlay a thin, stony sand layer which, in turn, overlay coral rubble. Examination of the surrounding area indicated that the profile described represented the maximum

soil development in that part of the islet. Frequently patches of coarse light grey (10 YR 8/2 dry) sand up to 30 cm thick were observed with no evidence of soil development. On moving inland, an area of soils showing significantly different vegetation was observed (dominance of grasses). This Profile 11, consisted of a silty dark brown

surface layer (10–15 cm) overlying coarse sand to a depth of at least 1 m. The surface layer was dominated by grass roots. The lower portions of the profile (below 40 cm) were permanently saturated with groundwater that moves under the influence of the tides to within 10 cm of the soil surface), and on digging into the layer below 40 cm, there was a sulfurous odor.

Profile 10 lies further toward the lagoon, and has a well-developed A horizon varying from 15 to 20 cm in depth overlying a CA horizon with minimal organic content and soil structure to about 30–35 cm. There is again evidence of groundwater variation, but the maximum depth of movement up the profile is about 75 cm. Further to the lagoon side, Profile 9, lies in a mid-islet ridge position in slightly convex, undulating terrain. This profile, formed on sand that changes from medium to coarse with depth, has a clearly developed A horizon, 15–20 cm deep with weakly developed granular structure. This organic-rich (10% organic carbon) layer overlies structureless medium and coarse sand to a depth of more than 1 m, with no contact with the groundwater being observed.

Profile 8 lies on a second sand ridge up from the lagoon, and has a clearly developed A horizon with more than 10% organic carbon to a depth about 10 cm. This overlies a lower organic content layer (approximately 10–20 cm depth), and then there is a buried A horizon (approximately 20–30 cm depth) with significantly lower carbon content (1.6%), which in turn overlies at least 1 m of stony coarse sand. The buried A horizon resembles surface soils in more disturbed parts of Tarawa (Seru and Morrison, 1985). On the sand terrace closest to the lagoon lies Profile 7. This has a very weakly developed soil profile, showing a thin (<10 cm) A horizon, with a layer below this showing minimal organic matter incorporation to a depth of 30 cm, lying on top of coarse sand to a depth of more than 1 m. Groundwater influences were noted from about 80 cm down and the groundwater (slightly brackish) was contacted at about 90 cm.

Thus, on moving across an islet of about 650 m width, there is evidence of five different soils, with the properties being influenced by depth to rock, particle size of dominant materials, organic matter content, soil structure, and influence of groundwater. In terms of soil classification (Soil Survey Staff, 1975, 1999), all the soils would be Entisols (or Regosols or Lithosols), i.e., recent soils with minimal profile development, with separation at different hierarchical levels depending on the soil properties listed above.

Near the southern island of Abatao, a profile was observed that met the requirements for classification as a Mollisol (Soil Survey Staff, 1999) in that it had a deep (>50 cm), dark colored (Munsell color values 3 or less), high base status (base saturation >50%) surface layer having some structural features. This is most unusual, as Mollisols are typically the rich, productive soils of the Great Plains of North America. Their presence on Abatao further confirms the wide range of properties that can be found on low elevation coral structures.

Another area of Abatao also showed the presence of the Jemo series soil first identified by Fosberg (1954, 1957). These soils have laminated subsurface layers formed of carbonate materials cemented by phosphatic material believed to be derived from reaction between guano from birds nesting in the surrounding *Pisonia* trees and the underlying carbonate substratum. This genetic process has yet to be confirmed experimentally.

Such diverse combinations of soils have been observed on other low elevation coral structures in other islands of Kiribati (Jenkin and Foale, 1968; Woodroffe and Morrison, 2001; Morrison and Woodroffe, 2009), Tuvalu (Morrison 1990), Cook Islands (Bruce, 1972), Marshall Islands (Stone, 1951; Fosberg, 1956), Solomon Islands (Wall and Hansell, 1976), French Polynesia (Tercinier, 1956, 1969; Jamet, 1985), Hawaii (Foote et al, 1972), and Maldives and Aldabra (Spaull, 1979).

Soils derived from carbonate materials have a wide range of uses despite their limitations. Such materials are the only soils in several island groups (Tuvalu, Maldives) and are common soils in other groups (Cook Islands, several Caribbean Islands). Inhabitants of these islands have developed agricultural practices to produce a wide range of crops on such soils. These include coconuts, pandanus, breadfruit, citrus, and vegetables, with the specific practices and crops dependent on local factors, including the rainfall pattern. The use of mulches and pits dug down to the water table (e.g., see Figure 3) are among the practices utilized to achieve significant production (Small 1972; Chase 1992).

### Physicochemical and mineralogical properties of low elevation coral soils

#### Physicochemical properties and plant nutrition

Many of the properties of low coral structure soils are related to the organic matter content of the topsoil. Topsoil organic carbon values vary from about 1% to 20% depending on the age of the soil, the vegetation, climate, and soil management. In subsoils, organic carbon values



**Soils of Low Elevation Coral Structures, Figure 3** *Cyrtosperma* sp. ("Babai") planted in the water table in a pit dug into soils on Bonriki, Tarawa, Kiribati.



are always low (<0.5%) unless there has been considerable soil disturbance, e.g., due to the digging of *Cyrtosperma* pits. Nitrogen values usually follow the organic contents closely, and C:N ratios usually range from about 5–15 for topsoils to 8–20 for subsoils. Water retention against 1500 kPa (15 bar  $\approx$  wilting point) pressure is often closely correlated with organic matter content; values of 5–25% have been obtained for topsoils, while for subsoils the values are always low (1–4%). Cation exchange capacity is also closely related to organic matter for topsoils, with values in the range 6–60 cmol/kg, while the values for the sandy calcareous subsoils are usually less than 5 cmol/kg. Exchangeable magnesium values are generally around 3–8 cmol/kg, sodium contents are about 0.2 cmol/kg, unless there has been saltwater intrusion, but exchangeable potassium values are always low (<0.1 cmol/kg) unless there are substantial organic matter contents.

The calcium carbonate content is always high, ranging from 55% to 90% for topsoils and usually being greater than 90% for subsoils. This dominance of the environment by carbonate leads to high pH values; pH (water) values for topsoils are usually in the range 7.1–8.5 and for subsoils 7.5–9.0; pH (CaCl<sub>2</sub>, 0.01 mol/L) values usually range from 7.0 to 8.0 for topsoils and from 7.5 to 8.0 for subsoils. Extractable phosphorus (Olsen et al., 1954, procedure) values are generally low (5–15 mg/kg) for topsoils and very low (<1 mg/kg) for subsoils, but can be higher (>50 mg/kg) at sites with guano accumulation. The total phosphorus contents vary considerably, ranging from 500 to 50,000 mg/kg for topsoils and from 100 to 5000 mg/kg for subsoils. Total sulfur values are fairly constant at around 4000 mg/kg.

Thus it can be seen that in the low coral islands the soils are alkaline, with most of the soil “fertility” related to the accumulated organic material. Under these conditions, nitrification is favored but toxic accumulations of nitrate are unlikely unless there are unusual hydrological conditions. Volatilization of nitrogen as ammonia from ammonium and urea fertilizers will occur, with particularly large losses occurring if these materials are not incorporated. The availability of phosphorus is controlled by calcium activity; much fertilizer P will be precipitated as calcium phosphates or adsorbed on the surfaces of the carbonates. K availability is decreased by high Ca and/or Mg levels; the low levels of K in the coral limestone parent materials mean that this element will always be in short supply.

Supplies of available Ca and Mg are plentiful in low elevation coral soils but imbalances with K and micronutrients cause significant plant nutrition problems. Sulfur is usually available in small quantities from solution of limestone and from rainwater, but if crops with large S requirements are grown intensively, external additions will be required. Solubilities of Cu, Fe, Mn, and Zn decrease with increasing soil pH. Cu deficiencies are less related to soil pH than to the other micronutrients. Zn forms relatively insoluble zincates in calcareous soils and Fe uptake is reduced by high bicarbonate

concentrations in the soil solution. With the relatively low contents in coral limestone, all of these elements are likely to be highly deficient in low elevation coral soils (Deenik and Yost, 2006; Morrison, 1992).

### Mineralogy

As the soils of the low elevation coral structures are dominated by calcium carbonate, the dominant minerals are calcite and aragonite, which are the common forms of calcium carbonate deposited by reef-forming and reef-living organisms. Calcite contains varying amounts of magnesium (substituting for calcium in the mineral structure). If the magnesium content is >1%, the mineral is described as high magnesium calcite (HMC); other forms are referred to as low magnesium calcite (LMC). Variations in the relative aragonite/HMC/LMC contents depend on the origin of the carbonate material base for the soils. For example, Hammond (1969) found on Kiritimati (Kiribati) that aragonite was the dominant component, this mineral being present in the greatest amounts in the coarse fragments. Calcite was more abundant where foraminifera dominated the deposits. Most calcite was high in magnesium but LMC was present mainly in the coarse sand, very fine sand, and silt fractions. Aragonite, which forms the hard parts of corals or algae, and HMC from algal skeletal material, are more abundant in most shallow water marine environments than LMC, but among deep sea oozes rich in calcitic foraminifera and coccoliths, the more thermodynamically (under Earth-surface conditions) stable LMC is the predominant phase (Chave, 1962). In soils where guano deposits have been incorporated, apatite is usually found.

### Conclusions

Soils of low elevation coral structures around the globe display many similarities. The soils usually show minimal profile development, and are highly calcareous and heavily dependent on organic matter for moisture, nutrient retention and availability. Despite the limited variation in soil-forming factors, a range of soil profiles has been observed with organic matter content, particle size, depth to rock, and the influence of groundwater, leading to differences in profile features and potential utilization of the soils. The soils are usually classified as Entisols (Regosols or Lithosols), the major differences being in the soil moisture regime and the particle size class. Micronutrient and potassium deficiencies are encountered widely.

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## Cross-references

Atolls

Coral Cays, Vegetational Succession

Low Wooded Islands

Vegetated Cays

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## SOLUTION PROCESSES/REEF EROSION

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## Definition

Calcium carbonate is soluble in water containing carbon dioxide, and thus, there has been focus on the chemical processes that take place in water, given the term “solution processes.” However, much erosion of calcium carbonate found in reef situations is actually effected by biological and mechanical processes, hence the wider term “reef erosion” is used to cover the range of processes involved.

## Solution processes

Much interest has been expressed in the question of whether or not limestones can be dissolved in seawater. The crux of the issue is that chemical analyses of surface seawater in open areas around reefs usually show that the waters are not frequently acid (with a pH often around 8.2) and are saturated with respect to calcium carbonate. If this is so, then it is difficult to envisage how calcium carbonate can move into solution in seawater from limestones (conversely, of course, it helps facilitate explanations of the formation of carbonate rocks by processes involving chemical precipitation). However, in intertidal situations, delicate, sculptured rock surface occur which, by analogy with freshwater situations, would appear to owe their origin to solution processes. An observer might conclude that these surface forms are produced by processes other than solution (for example, salt weathering or biological action), and the analogy with freshwater solution forms is both misleading and fortuitous. Alternatively, the conclusion can be that there are actually solution processes which facilitate the dissolution of limestones in

Solution Processes/Reef Erosion, Table 1 Erosion rates of reefs and reef limestones

| Locality                                   | Substrate      | Erosion type/agent            | Rate                                                        | Author                          |
|--------------------------------------------|----------------|-------------------------------|-------------------------------------------------------------|---------------------------------|
| <i>(a) Reefs</i>                           |                |                               |                                                             |                                 |
| Bermuda                                    | Reef           | Fish                          | 2–3 t ha <sup>-1</sup>                                      | Bardach (1961)                  |
| Bermuda                                    | Reef           | Fish, <i>Cliona</i>           | 1.3 mm a <sup>-1</sup>                                      | Bromley (1978)                  |
| Mariana Islands Atoll                      | Reef           | Fish                          | 1.1–1.6 t m <sup>2</sup> a <sup>-1</sup>                    | Cloud (1959)                    |
| Orpheus Island, Great Barrier Reef         | Reef           | <i>Tridacna crocea</i>        | 100 cm <sup>3</sup> m <sup>2</sup> a <sup>-1</sup>          | Hamner and Jones (1976)         |
| Florida                                    | Reef           | <i>Cliona</i>                 | 746 = 4,303 mm <sup>3</sup> reworked                        | Hein and Risk (1975)            |
| Florida                                    | Reef           | Bioerosion esp. <i>Cliona</i> | 1 m coral head in 150 years                                 | Hudson (1977)                   |
| Barbados                                   | Fringing reef  | <i>Cliona</i>                 | 80–377 g m <sup>2</sup> a <sup>-1</sup>                     | Stearn and Scoffin (1977)       |
| Pacific                                    | Reef lagoons   | <i>Echinoderms</i>            | 4.6 kg m <sup>2</sup> a <sup>-1</sup>                       | Bak (1990)                      |
| Great Barrier Reef                         | Reef           | dead <i>Porites</i>           | 1–8 kg m <sup>2</sup> a <sup>-1</sup>                       | Osorno et al. (2005)            |
| Model values                               | Reef           | <i>Echinoderms</i>            | 1.2 kg m <sup>2</sup> a <sup>-1</sup>                       | McClanahan (1995)               |
| Model values                               | Reef           | Grazing fish                  | 0.17 kg m <sup>2</sup> a <sup>-1</sup>                      | McClanahan (1996)               |
| Red Sea                                    | Reefs          | Sponges                       | 0.84 kg m <sup>2</sup> a <sup>-1</sup>                      | Zundevich et al. (2007)         |
| <i>(b) Reef limestones – bioerosion</i>    |                |                               |                                                             |                                 |
| Barbados                                   | Beachrock      | <i>Echinometra</i> boring     | 9–14 cm <sup>3</sup> a <sup>-1</sup>                        | McLean (1967)                   |
| Barbados                                   | Beachrock      | Gastropod grazing             | 1–2 mm a <sup>-1</sup>                                      | McLean (1967)                   |
| Barbados                                   | Beachrock      | Chiton grazing                | 8–13 cm <sup>3</sup> a <sup>-1</sup>                        | McLean (1967)                   |
| Heron Island, Great Barrier Reef           | Beachrock      | Chiton grazing                | 18 cm <sup>3</sup> a <sup>-1</sup>                          | McLean (1967)                   |
| Virgin Islands                             | Reef limestone | Sponge Boring                 | Up to 7 kg m <sup>2</sup> a <sup>-1</sup>                   | Moore and Shedd (1977)          |
| Bermuda                                    | Eolianite      | <i>Cliona</i>                 | 1.0–1.4 cm a <sup>-1</sup>                                  | Neumann (1966)                  |
| Great Barrier Reef                         | Beachrock      | <i>Lithophaga</i>             | 1.5 cm a <sup>-1</sup>                                      | Otter (1937)                    |
| Aldabra                                    | Reef limestone | <i>Lithophaga</i>             | 0.9 cm a <sup>-1</sup>                                      | Trudgill (1976)                 |
| Aldabra                                    | Reef limestone | <i>Lithotrya</i>              | 0.8 cm a <sup>-1</sup>                                      | Trudgill (1976)                 |
| Oman                                       | Reef limestone | <i>Lithophaga</i>             | 0.25 cm a <sup>-1</sup>                                     | Vita-Finzi and Cornelius (1973) |
| <i>(c) Reef limestones – overall rates</i> |                |                               |                                                             |                                 |
| Puerto Rico                                | Reef limestone | Intertidal notch              | 1.0 mm a <sup>-1</sup>                                      | Kaye (1959)                     |
| Red Sea                                    | Reef limestone | Intertidal                    | 1.0 mm a <sup>-1</sup>                                      | MacFadyen (1930)                |
| Bikini Atoll                               | Beachrock      | Intertidal                    | 0.3 mm a <sup>-1</sup>                                      | Revelle and Emery (1957)        |
| S.W. Australia                             | Reef limestone | Intertidal                    | 270–670 cm <sup>3</sup> a <sup>-1</sup> 100 cm <sup>2</sup> | Revelle and Fairbridge (1957)   |
| Grand Cayman                               | Reef limestone | Intertidal                    | 0.99 mm a <sup>-1</sup>                                     | Spencer (1985)                  |

seawater but which are not revealed by routine standard chemical analyses of open seawater. Geomorphological research has shown that both these possibilities can be true.

When inshore waters and intertidal rock pools are studied, this reveals that their chemistry can be substantially different to that of the open ocean. In particular, inshore waters in mangrove areas may actually become acidic if a peat substrate accumulates giving rise to significant solution erosion of limestone exposed in mangrove areas. More widely, in intertidal pools or other situations of closed or restricted water circulation, the existence of respiring organisms can substantially increase the amount of carbon dioxide in solution, and, therefore, the increasing potential for the dissolution of reef limestones. Emery (1946) showed that this will be especially the case at night when respiration output of carbon dioxide will not be balanced by photosynthetic uptake of carbon dioxide. Hence, solution of limestones is made possible in sea water due to biological respiration processes.

This may become more relevant in relation to future projections concerning atmospheric conditions and climate change. Recent work on the erosion of coral reefs

has focused on modeling the possible roles of climate change in reef erosion. This has discussed the effects of not only a rise in sea surface temperature (Sheppard, 2002; Carpenter et al., 2009) but also of acidification (Hoegh-Guldberg et al., 2007).

### Other erosion processes

While there has been considerable interest in the solution erosion of reefs and reef limestones, investigation has often revealed that some of the most powerful forces shaping the landforms involve biological erosion. However, this has sometimes been to the neglect of the processes common to all coasts, especially the physical processes. The wide range of processes which should be considered include wave action, wetting and drying, spray impact, abrasion by sand and pebbles, salt weathering and hydration, as well as solution and biological processes.

### Biological erosion

For the biological processes, both direct biological actions, such as grazing and boring by mollusks, and indirect actions, such as the alteration of carbonate chemical



equilibria, may be involved. Indeed, where dissolution processes appear to be important, this is usually in association with biological processes.

Many marine mollusks and other organisms graze algae, which are growing on or just within the rock surface. These grazers include mollusks such as Chitons, and gastropods with a rasping radula and fish. Other organisms bore into the reefs and reef limestones, including algae, sponges (especially *Cliona* and *Pione* species), bivalve mollusks (such as *Lithophaga*), barnacles (*Lithotrya*), and echinoderms (e.g., *Echinometra* species (Trudgill, 1985, pp. 137–155).

Bioerosion rates can be of the order of  $1\text{--}5\text{ kg m}^{-2}\text{ a}^{-1}$  (Table 1). Additionally, while Bak (1990) showed that bioerosion by sea urchins (echinoderms) in Pacific coral reef lagoons involved the direct destruction of  $12.5\text{ g m}^{-2}\text{ d}^{-1}$  ( $4.562\text{ kg m}^{-2}\text{ a}^{-1}$ ), Bak (1994) also showed that this can have an effect of weakening the reef structure. McClanahan (1995) calculated model values from published data of echinoid erosion of  $3.28\text{ g m}^{-2}\text{ d}^{-1}$  ( $1.197\text{ kg m}^{-2}\text{ a}^{-1}$ ) as compared to  $0.1699\text{ kg m}^{-2}\text{ a}^{-1}$  bioerosion by grazing fish.

## Zonation

Many of the processes of erosion of reef limestones are at their most powerful in the mid-intertidal: for example, wetting and drying cycles will decrease in number both upshore and downshore in relation to tidal cycles, upper shores being wetted and lower shores being exposed to drying only at extreme high spring tides. Other processes, for example abrasion, may be at a maximum in the lower shore, leading to planation at that level. However, for reefs themselves, where much of the erosion is biological, the focus of bioerosion is subtidal. In addition, sea levels have not been constant and the roles and erosion at higher and lower levels than at present have also to be taken into account in explaining present-day morphology.

## Exposure, process, and erosion rates

Whatever the erosion processes, exposure is a key factor. On the more exposed shores the relative importance of physical actions increases and this may be at the expense of biological processes. Trudgill (1976) showed that intertidal erosion rates of reef limestones on Aldabra Atoll, Indian Ocean, ranged from around  $1\text{ mm a}^{-1}$  on sheltered coasts where biological erosion dominated to  $4\text{--}5\text{ mm a}^{-1}$  on exposed coasts where physical wave action increased in significance. Similarly, Spencer (1985) showed that while reef limestones on Grand Cayman, West Indies eroded at a mean rate of  $0.99\text{ mm a}^{-1}$  the rates ranged from  $2.77\text{ mm a}^{-1}$  on sheltered coasts to  $2.77\text{ mm a}^{-1}$  were exposed. Further rates of erosion and their associated agencies are shown in Table 1.

## Summary

Earlier research focused on the relative importance of the differing erosion rates and clearly showed that biological

processes often dominate the erosion processes. This work was largely on growing reefs or reef limestones. The outlook is that more work will focus on the erosion of reefs following the deterioration of coral colonies in relation to increased anthropogenic sediment inputs and climate change.

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## Cross-references

[Algae, Blue-Green Boring](#)  
[Climate Change and Coral Reefs](#)  
[Echinodermata](#)  
[Ecomorphology](#)  
[Geomorphic Zonation](#)  
[Notch and Visor](#)

## SOLUTION UNCONFORMITIES

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### Definition

Horizons within coral reef formations which have been exposed to the atmosphere during low sea level phases and display distinctive chemical weathering features.

The term *solution unconformity* was first coined by Schlanger (1963) as part of the landmark work on the drilling of Enewetak Atoll and referred to weathered unconformities produced within the atoll succession, at

approximately 33, 330, and 930 m. The unconformities exhibit characteristics that might develop on exposed limestone surfaces, and they are also rich in mangrove pollen. Similar characteristics occur in drill core from Bikini (Ladd et al., 1953, 1970; Ladd and Schlanger, 1960) and Midway (Lincoln and Schlanger, 1987). Later surveys discovered a series of solution unconformities caused by atoll-wide emergence events tied to variations in relative sea level (Quinn and Matthews, 1990; Wardlaw and Quinn, 1991). In the upper 371 m of the atoll, nine major unconformities have been recognized, six of which are within the Pliocene–Pleistocene. The unconformities are the result of atoll emergence (fall in sea level) with resultant development of chemical erosion as a result of meteoric dissolution of the limestones. Surface effects include soil and calcrete development and various degrees of surface karstification at small (karren) to large (solution rims, dolines conical, and tower features) scales. Below the surface, distinctive dissolution and precipitational fabrics and specific chemical signatures occur (James and Choquette, 1988). Upon re-submergence, this surface is preserved as a solution unconformity which can be identified by petrographic characteristics and a distinctive stable isotope signature. In drill core, criteria used for identifying solution unconformities include soil and caliche development, mineralogic and chemical changes (including isotopic changes), fabric changes, and color changes (development of red-brown color). Further, due to the fact that porosity development below and above the solution unconformity is different, unconformities exhibit velocity differences imaged on seismic data (Purdy, 1974; Davies, 1974; Harvey et al., 1979).

In the Great Barrier Reef, four unconformities have been identified at Heron Island (Davies, 1974), while six have been identified at Ribbon 5 (northern Great Barrier Reef) and representing low stands in the past 350,000 years (Webster and Davies, 2004). A special example of solution unconformity is that which occurs at the base of modern reefs and separating the reef from their foundations. Called the Thurber discontinuity (Thurber et al., 1965), it defines a hiatus between Holocene reefs dated by radiocarbon and underlying Pleistocene reef limestones dated by Uranium-series methods as Last Interglacial in age. This hiatus represents nearly 100,000 ka of exposure. In most reef systems, solution unconformities may represent exposure on more than one occasion.

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## Cross-references

Antecedent Platforms  
Barbados  
Calcrete/Caliche  
Diagenesis  
Dolomitization  
Emergent Reefs  
Makatea  
Solution Processes/Reef Erosion

## SPICULITE

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Spiculite is a relatively uncommon inclusion within the framework of coral reefs. It is formed from cemented spicules or sclerites found within the mass of either soft corals, especially Alcyonarians (Konishi, 1982; Alderslade and Fabricius, 2009) or sponges – the sclerosponges – usually at depths below active coral growth (Hartman, 1977; Hooper, 2009).

Most sponges contribute little to the sediments which become incorporated in reef rock. However, the massive aragonite skeletons of sclerosponges help to strengthen and build out the walls of caves and cryptic locations. The demosponges also secrete siliceous spicules with varying admixtures of fibrous materials, but the amount released to reef sediments is relatively small (Hartman, 1977). In contrast, the basal stalks of alcyonarians, especially the genus *Simularia*, which become consolidated through submarine cementation of densely concentrated coenenchymal spicules are attached firmly to the

substratum. Locally they form uniformly composed lenses, up to centimeters in thickness which may be encountered in cores from reef drilling (Konishi, 1982). Most sclerosponges have been reported to be aragonite, but some magnesium calcite species have also been found (Milliman, 1974).

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## Cross-references

Octocorallia  
Sponges

## SPONGES

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## Synonyms

Porifera

## Definition

The simple, homogeneous structure of sponges (Phylum Porifera) distinguishes them from all other animals. They have no organ systems for reproduction, respiration, circulation, excretion, and digestion, and they are capable of extensive internal rearrangements in response to changed circumstances (e.g., Hartman and Reiswig, 1973; Bergquist, 1978, 1994). The resulting morphological versatility confers on sponges exceptional ability to recover from damage, propagate asexually, and develop symbiotic associations with a wide variety of plants, animals, and microbes. Sponges are also distinguished by astonishing biochemical diversity and novelty, with sponge metabolites accounting for nearly half of those reported from invertebrates (e.g., Harper et al., 2001). Sponges feed primarily on ultraplankton that they filter from water, as they pump it through a unique internal canal system, and many



species benefit from microbially mediated diet augmentation. Sexual reproduction involves release of sperm, or of both sperm and eggs, depending on the group; and the resulting larvae disperse relatively meager distances (Zea, 1993; Rützler, 2004; Maldonado, 2006).

### Sponges of coral reefs and linked ecosystems

On coral reefs, sponge biomass can exceed coral biomass, and sponges exhibit extreme diversity of growth forms (encrusting, massive, tubes, vases, bushes, runners, plates), sizes (a few mm to more than 2 m), and colors (every hue) (e.g., Diaz and Rützler, 2001; Wulff, 2001). Species diversity of sponges can be an order of magnitude greater than coral diversity. Van Soest (1994) compiled records of 640 species from the Caribbean, 259 from the Red Sea, 450 from the central Indian Ocean, 965 from Indonesia, and 717 from tropical Australia, and he directed attention to gaping holes in geographic distributional data. In a comprehensive biodiversity study of tropical Australian sponges, Hooper et al. (2002) corroborated the extreme geographic and habitat heterogeneity in sponge faunal composition reported in previous studies and estimated that fewer than 30% of sponge species are described. Taxonomic and quantification challenges pervade studies of all aspects of sponge ecology. Identification at least to genus is crucial because of the great variation among sponge species in functional roles. Abundance and individual size are best quantified by volume because many roles are played out in proportion to volume of living tissue (e.g., Wulff, 2001). Beneficial contributions of sponges to coral reefs and associated ecosystems include: efficient filtering of prokaryote plankton from the water column; binding living corals to the reef frame; facilitating reef regeneration; protecting mangrove prop roots and reef corals from invasion by boring organisms; providing food for charismatic animals such as hawksbill turtles, angelfishes, and nudibranchs; regenerating nutrients and adding to primary production through symbiotic microbes with special biochemical capabilities; harboring symbionts of virtually every animal phylum, as well as many algae, protists (including zooxanthellae), and prokaryotes; and attracting support for responsible human stewardship with aesthetically appealing colors and shapes (e.g., Rützler, 1978; Diaz and Rützler, 2001; Wulff, 2001).

### Filtering the water column

Sponges pump water through an internal canal system that is punctuated by chambers lined with flagellated cells, filtering out food and exhaling water that has been profoundly altered. By comparing incoming and outgoing water, and computing sponge energy budgets, Reiswig (1971, 1974, 1981) demonstrated extreme efficiency at removing particulate organic material of bacterial size range and discovered that sponges hosting large internal populations of bacteria ("bacteriosponges") could meet a significant portion of their metabolic needs by uptake of

dissolved organic material. Studies using recent technological advances to build on this foundation have determined that sponge feeding can be influenced by the following characteristics of the sponges and their environments: sponge internal morphology (body wall thickness, canal lengths and widths, density of choanocyte chambers), sponge size and shape (e.g., height above the substratum, ability to inhabit cryptic spaces), sediment in the water column (causing sponges to cease pumping or clog), symbionts (cyanobacteria and zooxanthellae that share food, bacteria that facilitate uptake of DOC, and macroscopic symbionts that can interfere with pumping), and concentration and types of plankton (e.g., heterotrophic bacteria, cyanobacteria, prochlorophytes, picoeukaryotes) in the environment (e.g., Reiswig, 1974; Pile, 1999; Yahel et al., 2003; Lesser, 2006; and a review in Rützler, 2004). Much remains to be learned of the overall balance of sponge influences on the water column, but it is clear that reduced water quality will result if sponges are diminished or lost from tropical and subtropical coastal habitats. Reiswig (1974) calculated that the sponges on the Jamaican fore-reef slope could fully filter the entire water column every 24 h, and by estimating the overall water column influence of sponges in Florida Bay, Peterson et al. (2006) concluded that a series of ecosystem-perturbing cyanobacteria blooms could be entirely explained by losses of sponges from many areas within the bay.

### Reef-building and rebuilding, carbonate balance, and coral survival

Sponges exert enormous influence on living corals and the reef framework, in an assortment of positive and negative roles that depend on sponge morphology, symbionts, and capacity to erode carbonate. Several species of coralline sponges add their solid aragonitic skeletons to caves, cryptic spaces within the frame, and deep reefs, where their independence from sunlight boosts their importance as carbonate accretors; but in general, sponge skeletons add little new solid material to recent reefs. Skeletons of non-coralline Demospongiae, the class to which most coral reef sponges belong, are typically composed of silica spicules and/or fibers of the protein spongin, and they disintegrate when not embedded in living tissue. A handful of sponge species in the orders Hadromerida and Haplosclerida rework solid carbonate into fine sediment (Hartman, 1977; Rützler, 2002). Silt-sized chips, created as they excavate burrows, infill cavities in the reef frame, where subsequent lithification cements permanently. On the negative side, the excavations weaken basal attachments of living corals, increasing their susceptibility to being disengaged from the reef frame and perishing in the surrounding sediments. Boring sponge abundance and activity may be promoted by elevated water column nutrient levels (e.g., Holmes, 1997), and details of the interaction boundary between the coral and sponge can substantially influence the excavations (e.g., Schönberg, 2003; López-Victoria et al., 2006).

Where coral skeletons are bared of living tissue, they are especially vulnerable to excavators. Goreau and Hartman (1966) pointed out that sponges growing over exposed carbonate can help protect against excavation, and that sponges can hold living corals in place even after their own skeletal attachments to the reef frame have been completely eroded (Hartman, 1977). Fore-reef patch reefs from which all sponges, except excavating and encrusting species, were removed suffered ten times the coral losses of control patches which retained their sponges (40% vs. 4% of corals lost) in only 6 months (review in Wulff, 2001).

Carbonate rubble can be regenerated into living reef if it is stabilized sufficiently for corals to colonize and survive. Sponges are able to quickly bind multiple pieces of rubble together, providing the stability required for carbonate-secreting organisms, such as encrusting coralline algae, to consolidate the rubble by growing between rubble pieces (Wulff, 2001). Carbonate sediments can also be bound by sponges (review in Rützler, 2004). Sponge-binding can make the difference between success and failure of reef regeneration in shallow zones, where rubble is otherwise continuously moved, and this process can prevent losses to gravity on deep talus slopes (Hartman, 1977). Under some circumstances, adding sponge fragments to rubble piles may be a low-cost, aesthetically appealing, and ecologically sustainable method of restoration for damaged reefs.

Demonstrated positive effects of sponges on corals mandate cautious interpretation of apparent overgrowth of corals, unless observations have been made in time series. Most confirmed coral overgrowths by sponges involve encrusting or excavating species, many of which are fueled in part by photosynthetic symbionts. Although only a few of the hundreds or thousands of sponge species in each of the regional coral reef faunas have been observed to overwhelm corals, local effects can be dramatic with respect to the areal extent of the infestation and the speed with which it occurs, and a variety of stresses, including temperature, sediment or other pollutants, and physical damage, may increase coral vulnerability to overgrowth (reviews in Rützler, 2002, 2004; Wulff, 2006c). Concern that loss of live corals to sponges may increase is bolstered by recent reports from Hawaii and the tropical eastern and western Pacific of invasions by nonnative species that can overgrow corals.

### Losses of sponges to disease, deteriorated water quality, and physical disturbance

Diseases of coral reef sponges appear to be increasing, but relevant data are rare. Because sponges disintegrate rapidly after death, particular individuals must be monitored over time in order to evaluate losses due to disease. Observations of disease prevalence require careful interpretation, as diseased sponges may recover. Most reports of significant losses due to disease have focused on large, conspicuous, or commercially valuable species, suggesting that many sponge losses are going unremarked

(Wulff, 2006a; Webster, 2007). Losses of up to 90% of the sponges at many seagrass sites in Florida Bay would never have been known if sponges had not been repeatedly monitored at those sites. In the sole study in which sponges have been repeatedly censused on a coral reef, half of the original 39 sponge species were lost in the course of only 14 years (Wulff, 2006a). Disease was implicated in at least some of these losses, but until additional sites are repeatedly censused, it is impossible to know how generally serious losses to disease and physiological collapse are.

Damage due to storms and other physical disturbances must be evaluated immediately after the disturbance, or with prior knowledge of the sponge communities, as damaged sponges can heal, and dead sponges vanish, within weeks. Amount of damage may not accurately indicate ultimate effects of disturbance for sponges. After a major hurricane in Jamaica, an inverse relationship between resistance to damage and recovery was revealed by monitoring sponges of 67 species for recovery or continued deterioration. A high proportion of massive sponges with tough skeletons resisted damage, but recovery was rarely successful for those that were damaged. By contrast, branching species suffered extensive damage, but recouped losses by reattaching as fragments (Wulff, 2006b).

High sponge species diversity, in combination with wide variation among sponge species in vulnerability to various abiotic stresses, renders sponges suitable for environmental quality monitoring in areas where sponge faunas have been studied well enough to interpret the patterns (e.g., Rützler, 2004; Alcolado, 2007).

### Spongivory

Relatively few animals are capable of consuming sponges, but predation has been demonstrated to constrain habitat or microhabitat distribution for some tropical species (review in Wulff, 2006c). Caribbean coral reef sponges are prevented from living in adjacent seagrass meadows by opportunistic feeding of seagrass-dwelling starfish, and mangrove species that are normally out of reach for reef-dwelling spongivores tend to be consumed when transplanted to coral reefs. Some sponge species inhabiting cryptic spaces within the reef frame, in the tropical western and eastern Pacific and in the Caribbean, are prevented from living on exposed surfaces by spongivores and normally herbivorous parrotfishes. By contrast, spongivores that routinely consume sponge species typical of their habitat do not appear to eliminate them, and some of the sponge species most frequently consumed remain the most abundant. Sponge specialists feed on sponge species with which they coexist in different ways. Nudibranchs may specialize on particular sponge species. Hawksbill turtles consume large quantities of only a handful of species in 3 of the 13 extant demosponge orders. Angelfishes instead feed in what has been termed smorgasbord fashion, with fish tending to consume small amounts of each of many sponge species (e.g., 70 species in gut contents; and direct observations of consumption of

23 species on a St. Croix reef and 64 species on a Panamanian reef). Palatability of a particular sponge species is predator specific, such that a species that is readily devoured by one predator, may be consumed in small portions by another, and completely rejected by others (review in Wulff, 2006c).

### Interactions with neighbors

Sponge overgrowth of sessile neighbors can be mediated by chemistry or growth rate and form, but time-series monitoring of apparent competitive interactions has often revealed that overgrowth is not progressing or that the net result is beneficial. Competitive interactions appear to be more likely to influence community composition in cryptic reef habitats and on mangrove prop roots. Sponges appear to be particularly good at tolerating, or even benefiting from, overgrowth by other sponges, and mutual benefit has been experimentally demonstrated for several cases of intimate heterospecific associations of tropical sponges (review in Wulff, 2006c).

### Symbiotic associations

The diversity, at all taxonomic levels, of symbionts hosted by sponges is extreme, but functional importance of intimate associations is not always understood. Sponges harbor a high diversity of bacteria, archaebacteria, and eukaryotic microorganisms (1694 16S rRNA sequences by the time of a review by Taylor et al., 2007), some of which have been shown to mediate carbon, nitrogen, or sulfur metabolism within sponges. The high proportion of phototrophic (i.e., obtaining at least half of their food from symbiotic cyanobacteria) sponges on the outer vs. inner Great Barrier Reef (GBR) and on the GBR vs. Caribbean reefs indicates how critical symbiont-mediated diet augmentation can be in oligotrophic water (Wilkinson and Cheshire, 1990).

Many hundreds of individual crustaceans, polychaetes, cnidarians, mollusks, fishes, echinoderms, and other animals have been discovered to be sheltering within a single sponge, and over a hundred species of inquilines have been found in representatives of a single sponge species. Sponges also grow over, or in tandem with, mangrove prop roots, a variety of colonial cnidarians, macroalgae, crustaceans, bivalves, and heterospecific sponges. Net results of symbioses range from mutualism to commensalism to parasitism and may be context dependent. Benefits traded by participants in mutualisms include protection against predators, substratum space, structural support, surface cleaning, inhibition of boring organisms, and nutritional collaboration (reviews by Rützler, 2004; Wulff, 2006c). Losses of sponges from tropical habitats would directly result in enormous additional biodiversity losses.

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## Cross-references

Binding Organisms  
Bioerosion  
Mangroves  
Reef Restoration  
Symbiosis; Zooxanthellae

## SPURS AND GROOVES

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### Definition

Spurs and grooves form a comb-tooth structure common to many coral reef fronts. Best developed on the windward side of reefs, the structure consists of elongate channels or grooves, a few meters wide and deep, separated by seaward-extending coral ridges or spurs (Figure 1) (Maxwell, 1968, p. 110). Grooves are commonly floored with coral rubble or carbonate sand. Where actively accreting, spurs are covered with living corals. Where accretion has ceased, spurs harbor associated benthic organisms (Shinn, 1963).

### Morphology

One of the most obvious of reef features that is found worldwide is the spur-and-groove system, finger-like

coral projections located on the seaward side of coral reefs. Early authors called the spurs buttresses or simply the buttress zone (Odum and Odum, 1955). These features, clearly visible in aerial images, are restricted mainly to the windward side of reefs at or near the break in slopes. They serve as living breakwaters, reducing the height and force of waves impinging on the most exposed portion of the reef (Munk and Sargent, 1948). Actively forming spurs often begin growth at the tidally exposed reef flat and may extend outward to water depths of up to 20 m. Spur corals are also “tuned” to the direction and degree of wave energy. In especially high-energy, large-wave regimes such as Pacific atolls, spurs are narrow and closely spaced, i.e., more spurs and grooves per unit area (Cloud, 1959). In lower-energy areas, such as in the Caribbean and the Florida Keys, spurs tend to be wider, whereas the grooves separating them may or may not be wider (Goreau, 1959; Shinn, 1963). This is especially true for offshore barrier and bank reefs with reef flats that remain submerged most of the time. Spurs and intervening grooves tend to be narrower on fringing reefs backed by a rocky shore or sea cliff (Cloud, 1959; Shinn et al., 1981).

Spurs may reach 8 m in height. About 4 m is typical in the Atlantic. Grooves may be scoured to bedrock in the Caribbean but are generally lined with carbonate reef sand and coral debris (Newell, 1958; Goreau, 1959; Shinn, 1963).

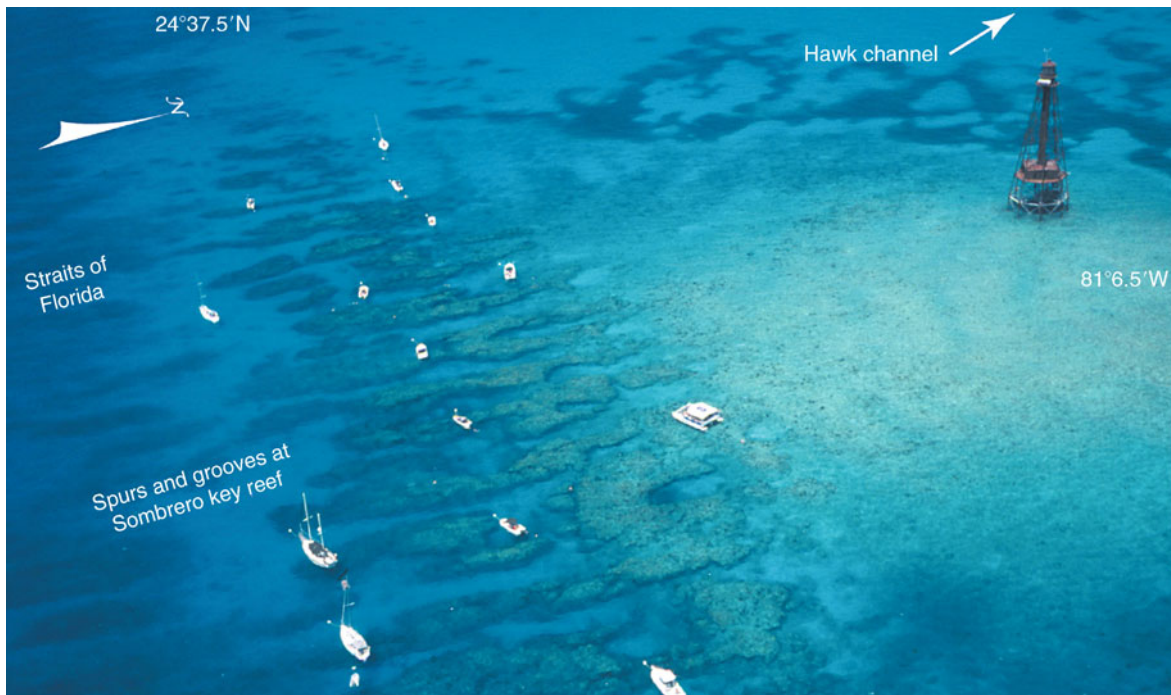
### Composition

Work in Florida shows that rapidly growing, oriented colonies of *Acropora palmata* constructed most spurs there (Shinn, 1963; Shinn et al., 1981; Lidz et al., 2007; Lidz et al., 2008). Branches in oriented colonies face either seaward into oncoming waves or landward away from oncoming waves in parts of the Caribbean (Goreau, 1959). On Florida bank reefs, the branches are oriented mainly away from oncoming seas (Shinn, 1963). Branches of unoriented colonies that extend toward and into adjacent grooves are usually broken off during heavy weather and wave action. Branches oriented away from incoming seas are the most resistant to breakage during both normal and heavy seas, such as during hurricanes (Ball et al., 1967).

Constructional spurs are tuned to the waves much like bristlecone pines in the wind-blown tundra or other trees growing in the areas of prolonged high winds. Some erosion does occur and aids in the formation of the system, but the spurs are primarily constructional features.

### Processes

In the Pacific and other areas of high-intensity waves, the grooves can be mainly erosional in origin (Cloud, 1959, and observations by the author). Around Pacific atolls, grooves are usually scoured clean and may contain circular potholes enclosing rounded coral boulders (Cloud,



**Spurs and Grooves, Figure 1** Spurs and grooves at Sombrero Key Reef in the middle Florida Keys offer a popular dive site. The spurs are no longer growing but nonetheless consist of colorful hardbottom communities. (Reprinted from Lidz et al., 2007, with permission.)

1959). During rough sea conditions, the boulders grind the pothole sides, like a mortar and pestle, thus enlarging the pothole while reducing the diameter of the grinding boulder. Potholes are less common in the Caribbean, and grooves are often sand-filled.

In addition to being tuned to wave-energy level, spurs and grooves are also tuned to wave direction (Munk and Sargent, 1948). Spurs usually have a normal alignment to incoming waves even if the waves have been refracted, such as those occurring along the rims of the circular atolls. On the sides of the atolls, spurs are oblique to the reef trend. Spurs are generally absent on the leeward side of atolls or carbonate banks. Grooves are eroded into whatever substrate may exist, whether it is coral or other material produced by reef and reef-flat growth. In such cases, living coral and other encrusting organisms may populate the spurs. Thus, Pacific spurs are both erosional and constructional in origin (Guilcher, 1958). Spurs are further strengthened by growth of encrusting coralline red algae and internal marine precipitation of both aragonite and high-magnesium calcite. Precipitation is hastened by wave-generated pumping of seawater, which increases the volume of seawater flowing through the reef. Seawater is the source of precipitated carbonate minerals.

Where growth is especially rapid, corals may grow laterally to produce overhangs. Such overhangs can completely bridge grooves, forming tunnels that can reach tens of meters in length. The tunnels can develop over both constructional and erosional grooves. Cryptic algal and

coral species grow on the roofs of such tunnels. Frequency of major storm waves are likely to control the development of tunnels. Many tunnels formed in this way may simply terminate at a blind end, or they may have an upward-directed “escape” tunnel that serves as a relief valve. The valves may act as “blowholes” during stormy weather.

Throughout the Caribbean and Florida, corals show clear evidence of former sea-level changes. Paleoshorelines formed by still stands of sea level are especially visible as parallel bands of lime sand in aerial images. Early Holocene reefs that did not keep pace with rising sea level are common. These deeper coral reefs generally originated as fringing reefs but are now 20–30 m below sea level (Banks et al., 2007). The spurs and grooves fronting these deeper fossil reefs generally are narrower and more abundant than those on the shallow bank reefs.

### Summary

Spur-and-groove structures always form on the windward side of coral reefs in response to unidirectional wave energy. Where wave energy is consistently high, as on the Pacific atolls, grooves are mostly erosional in origin. In areas of lesser wave energy such as in Florida and the Caribbean, the grooves are constructional with spurs growing on either side of sand- or rubble-filled channels. Florida and Caribbean spurs consist mainly of oriented branches of *Acropora palmata*. The most common, and wave resistant, orientation of *A. palmata* branches is

landward. A tunnel forms where corals are able to grow over grooves. If both ends of the tunnel remain open, the landward end can become a blowhole during storms.

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## Cross-references

[Acropora](#)  
[Atolls](#)  
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[Wave Shoaling and Refraction](#)  
[Western Atlantic/Caribbean, Coral Reefs](#)

## STABLE ISOTOPES AND TRACE ELEMENTS

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## Synonyms

Coral paleoclimatology; Geochemical tracers; Proxies

## Definitions

**Coral geochemistry:** The science of studying variations in the stable isotopic composition and trace element impurities in the calcium carbonate of coral skeletal material. The stable isotope and trace element geochemistry of coral carbonate reflects changes in the environmental conditions the coral is living in and/or the physiology of the coral.

**Stable isotope:** Two or more forms of a chemical element that have a different atomic mass. The isotopic forms of a particular element differ in the number of neutrons contained in the atom's nucleus. The term *stable isotope* refers specifically to the isotopic forms of a chemical element that do not undergo radioactive decay.

**Trace element:** Any element that is present in minute quantities, often substituting within a compound or crystal structure for a more abundant element that behaves in a similar fashion chemically.

## Overview

Massive corals in the reef ecosystems of the tropics provide some of the richest paleoclimate archives in the world. Corals are particularly useful paleoclimate recorders because they are widely distributed, can be accurately dated, and contain a remarkable array of geochemical tracers within their calcium carbonate (aragonite) skeletons. The suite of isotopic and elemental tracers in corals presently exceeds that developed for any other biogenic mineral phase. As a result, a multi-proxy approach to coral-based paleoclimatology is emerging that is yielding new insights into tropical paleoclimates (see [Paleoclimate from Corals](#)).

*Porites* is the most widely utilized genus in coral paleoenvironmental studies because it is common throughout the tropical Pacific and Indian Oceans, and individual colonies can live for up to ~400 years (see [Porites](#)). Reconstructions of even greater length are being developed using the longer-living and slower-growing genus, *Diploastrea*. In the Atlantic Ocean, coral reconstructions are commonly extracted from massive colonies of *Montastrea*, and to a lesser extent *Diploria*, which may also live for many centuries. Scleractinian corals from subtropical settings and the deep ocean are also being explored as recorders of environmental conditions (see [Cold Water Coral Reefs](#)). The following discussion will focus on environmental proxies in tropical reef-building corals.



Isotopic and elemental tracers in fossil corals preserved in submerged and tectonically raised reefs (see [Emergent Reefs](#); [Submerged Reefs](#)) offer a unique archive for defining the sensitivity of tropical climate to changing boundary conditions throughout the late Quaternary (the last ~500,000 years). Precise radiometric ages and internal chronologies for coral records are essential for integrating them with other high-resolution paleoclimate data derived from tree rings, ice cores, and varved sediments. Ages for fossil corals may be obtained by measuring U/Th with thermal ionization mass spectrometry (Edwards et al., 1987), with errors generally less than 1% for samples that

Diagenesis is a critical issue for coral paleoenvironmental studies (see *Diagenesis*, *Aragonite* and *Calcite*). Any secondary carbonate material that forms in the coral skeletal structure will alter the original isotopic and trace element signals and compromise the chemical record. To date, the effects of diagenesis have only been studied in detail for the main coral proxies (namely  $^{18}\text{O}/^{16}\text{O}$ ,  $^{13}\text{C}/^{12}\text{C}$ , and Sr/Ca). Overgrowths of inorganic aragonite precipitated from seawater and dissolution of coral aragonite produce cool artifacts in sea-surface temperatures (SSTs) reconstructed from coral  $^{18}\text{O}/^{16}\text{O}$  and Sr/Ca (e.g., Enmar et al., 2000; Müller et al., 2001; Hendy et al., 2007). In subaerial settings, freshwater diagenesis can lead to the precipitation of inorganic calcite within fossil coral skeletons. The relatively high Sr/Ca of calcite produces strong warm artifacts in coral paleotemperature records (McGregor and Gagan, 2003). In contrast, inorganic calcite precipitated from reactions involving tropical meteoric waters generally has an  $^{18}\text{O}/^{16}\text{O}$  composition similar to that found in coral aragonite. Corals can be screened for diagenesis using X-ray diffractometry

**Stable Isotopes and Trace Elements, Table 1** Summary of environmental factors controlling geochemical tracers in coral skeletons

| Tracer                | Environmental signals |                     |                     |                   |    |                     |           |                 |           |
|-----------------------|-----------------------|---------------------|---------------------|-------------------|----|---------------------|-----------|-----------------|-----------|
|                       | Temperature           | Rainfall/<br>Runoff | Light/<br>Turbidity | Ocean circulation | pH | Redox<br>conditions | Nutrients | Nuclear testing | Pollution |
| $\delta^{18}\text{O}$ | X                     | X                   |                     |                   |    |                     |           |                 |           |
| $\delta^{13}\text{C}$ |                       |                     | X                   | X                 |    |                     | X         |                 |           |
| Sr/Ca                 | X                     |                     |                     |                   |    |                     |           |                 |           |
| U/Ca                  | X                     |                     |                     |                   |    |                     |           |                 |           |
| Mg/Ca                 | X                     |                     |                     |                   |    |                     |           |                 |           |
| B/Ca                  | X                     |                     |                     |                   |    |                     |           |                 |           |
| Luminescence          |                       | X                   |                     |                   |    |                     |           |                 |           |
| Ba/Ca                 |                       | X                   |                     | X                 |    |                     | X         |                 |           |
| Cd/Ca                 |                       |                     |                     | X                 |    |                     | X         |                 | X         |
| Mn/Ca                 |                       |                     |                     |                   |    | X                   |           |                 |           |
| REEs                  |                       |                     |                     |                   |    | X                   |           |                 | X         |
| $\Delta^{14}\text{C}$ |                       |                     |                     | X                 |    |                     | X         | X               |           |
| Pb/Ca                 |                       |                     |                     |                   |    |                     |           |                 | X         |
| $\delta^{11}\text{B}$ |                       |                     |                     |                   | X  |                     |           |                 |           |
| P/Ca                  |                       |                     |                     |                   |    |                     | X         |                 | X         |
| $\delta^{15}\text{N}$ |                       |                     |                     |                   |    |                     | X         |                 | X         |

(for calcite), thin section analysis, and scanning electron microscopy (e.g., Bar-Matthews et al., 1993; Hendy et al., 2007; McGregor and Abram, 2008). The use of multiple coral records from similar time periods also serves to reduce potential errors in paleoenvironmental reconstructions (e.g., Hendy et al., 2002).

## Stable isotopes

### Oxygen isotopes

The use of oxygen isotope ratios in carbonate minerals as a paleothermometer began with Urey (1947), who showed that thermodynamic fractionation of  $^{18}\text{O}$  and  $^{16}\text{O}$  occurs during carbonate precipitation. Today, the majority of coral geochemical studies are based on measurements of oxygen isotopes because they are relatively straightforward to measure and interpret. Stable isotope ratios are expressed using a delta notation ( $\delta$ ), where  $\delta$  is the measured heavy isotope enrichment relative to a reference material expressed as a deviation in parts per thousand (‰). The  $\delta$  value for oxygen is defined by the equation  $\delta^{18}\text{O} = 1000(R_s - R_r)/R_r$ , where  $R_s$  and  $R_r$  are the  $^{18}\text{O}/^{16}\text{O}$  ratios of the sample and reference material, respectively. In oxygen isotope studies the term enrichment refers to an increased abundance of the heavier  $^{18}\text{O}$  atom, corresponding to a higher  $\delta^{18}\text{O}$  value.

The  $\delta^{18}\text{O}$  of coral aragonite reflects the temperature and  $\delta^{18}\text{O}$  value of seawater during coral growth. However, the symbiotic algae in the coral tissue enhance calcification rates, thus coral aragonite is depleted in  $^{18}\text{O}$  relative to aragonite precipitated in equilibrium with ambient seawater. McConnaughey (1989a, b) showed that kinetic isotope disequilibrium during the hydration and hydroxylation of  $\text{CO}_2$  produces simultaneous depletions of  $^{18}\text{O}$  and  $^{13}\text{C}$  in coral skeletons. The  $\delta^{18}\text{O}$  disequilibrium offset can differ between coral colonies, resulting in differences of up to 0.4‰ in mean  $\delta^{18}\text{O}$  (e.g., Linsley et al., 1999; Cobb et al., 2003; Felis et al., 2003). Multiple coral samples from similar time periods can be analyzed to reduce the uncertainty in interpreting differences in mean coral  $\delta^{18}\text{O}$  values (e.g., Cobb et al., 2003; Abram et al., 2009).

It appears that the  $\delta^{18}\text{O}$  offset for individual coral colonies generally remains constant over time and does not affect the interpretation of isotopic signals within single coral samples (e.g., McConnaughey, 1989a; Hendy et al., 2002). However, in rare cases where *Porites* coral extension rates are less than  $6 \text{ mm year}^{-1}$ , kinetic disequilibrium does affect coral  $\delta^{18}\text{O}$  (Felis et al., 2003). This growth effect has also been observed within individual coral colonies, where  $\delta^{18}\text{O}$  values tend to be higher on the shaded, slow-growing sides of colonies, or within valley structures (McConnaughey, 1989a; Allison et al., 1996; Cohen and Hart, 1997). Growth effects can be minimized by analyzing corals with extension rates exceeding  $6 \text{ mm year}^{-1}$  and by sampling for  $\delta^{18}\text{O}$  along major coral growth axes.

A common approach in early environmental reconstructions using coral  $\delta^{18}\text{O}$  (when other tracers were not analyzed) was to attribute the source of the isotopic variations primarily to a single factor. For example, at sites where the  $\delta^{18}\text{O}$  of seawater remains approximately constant, coral  $\delta^{18}\text{O}$  records have been used as a proxy for SST based on carbonate paleotemperature relationships (e.g., Epstein et al., 1953; Weber and Woodhead, 1972).  $\delta^{18}\text{O}$ -SST calibrations have been developed for several reef settings where variations in SST dominate changes in coral  $\delta^{18}\text{O}$ . The  $\delta^{18}\text{O}$ -temperature dependence for *Porites* corals is generally from  $-0.18\text{‰}$  to  $-0.22\text{‰}$  per  $1^\circ\text{C}$  (e.g., Weber and Woodhead, 1972; McConnaughey, 1989a; Gagan et al., 1994; Leder et al., 1996; Quinn et al., 1996; Wellington et al., 1996; Gagan et al., 1998; Suzuki et al., 1999; Felis et al., 2000; Juillet-Leclerc and Schmidt, 2001). A recent compilation of 14 coral  $\delta^{18}\text{O}$  records for the tropical Indian and Pacific oceans indicates that the late twentieth century was the warmest period in the tropics over the last 250 years (Wilson et al., 2006).

At other reef locations, changes in the  $\delta^{18}\text{O}$  of seawater override the influence of changes in SST on coral  $\delta^{18}\text{O}$ . Seawater  $\delta^{18}\text{O}$  varies in response to changes in the balance between precipitation, evaporation, and water advection. At sites where seawater  $\delta^{18}\text{O}$  correlates with rainfall, long coral  $\delta^{18}\text{O}$  records have been used to reconstruct precipitation patterns. Such records have been particularly useful for understanding the long-term history of intertropical convergence zone positioning and ENSO rainfall variability (e.g., Cole et al., 1993; Linsley et al., 1994; Tudhope et al., 2001; McGregor and Gagan, 2004).

A more powerful recent approach has been to determine SST variations using an independent coral proxy (such as Sr/Ca) and couple this with coral  $\delta^{18}\text{O}$  measurements to reconstruct both temperature and hydrological variations (e.g., McCulloch et al., 1994; Gagan et al., 1998; Gagan et al., 2000; Ren et al., 2002; Abram et al., 2007). The  $\delta^{18}\text{O}$  residual ( $\Delta\delta^{18}\text{O}$ ), obtained by removing the temperature component of the coral  $\delta^{18}\text{O}$  signal, can be used to make inferences about the hydrological cycle because  $^{18}\text{O}$  is fractionally distilled during the evaporation and precipitation of water vapor between the ocean and atmosphere. Advances in the analytical techniques for measuring trace elements in carbonates has meant that these multi-proxy studies are becoming more common, and there is less reliance on assuming a dominant SST or rainfall driver in interpreting coral  $\delta^{18}\text{O}$  records.

### Carbon isotopes

Carbon isotope ratios ( $\delta^{13}\text{C}$ ; representing  $^{13}\text{C}/^{12}\text{C}$ ) in coral aragonite are measured simultaneously with  $\delta^{18}\text{O}$  during the stable isotope analysis of  $\text{CO}_2$  and a large body of archived  $\delta^{13}\text{C}$  data is available. The interpretation of  $\delta^{13}\text{C}$  records from corals is not straightforward owing to the wide range of factors that modulate coral  $\delta^{13}\text{C}$ . The  $\delta^{13}\text{C}$  of coral aragonite reflects kinetic and metabolic

disequilibrium offsets, as well as variations in seawater isotopic composition (e.g., McConnaughey, 1989a; Swart et al., 1996). Seawater  $\delta^{13}\text{C}$  is controlled by the balance between primary production and respiration in the surrounding ecosystem, by air–sea exchange, and by mixing of surface and upwelled waters. In upwelling regions, nutrient-driven algal blooms can alter coral  $\delta^{13}\text{C}$  by preferentially removing  $^{12}\text{C}$  from seawater (Abram et al., 2003), and by changing the balance between the autotrophic and heterotrophic diet of the coral (Felis et al., 1998).

Coral  $\delta^{13}\text{C}$  is strongly influenced by metabolic fractionation due to coral respiration and endosymbiotic algal photosynthesis (e.g., McConnaughey, 1989b; Grottoli and Wellington, 1999). Endosymbiotic photosynthesis is generally the dominant influence on skeletal  $\delta^{13}\text{C}$  in hermatypic corals like *Porites* (McConnaughey et al., 1997). Photosynthesis depends to a large extent on ambient light levels, mediated by insolation, coral depth, and water column turbidity (e.g., Swart, 1983). At many sites, the seasonal cycle of cloudiness is in phase with coral  $\delta^{13}\text{C}$  cycles, with decreased photosynthesis leading to depletion of  $^{13}\text{C}$  in the coral skeleton (e.g., Goreau, 1977; Fairbanks and Dodge, 1979; McConnaughey, 1989a, b; Cole and Fairbanks, 1990; Winter et al., 1991; Shen et al., 1992). A decrease in skeletal  $\delta^{13}\text{C}$  also occurs in corals at increasing water depth, related to decreased light intensity and photosynthesis (e.g., Weber et al., 1976; Grottoli and Wellington, 1999). The metabolic influence associated with the annual coral spawning process has also been shown to produce distinct, short-lived  $^{13}\text{C}$  enrichments in coral  $\delta^{13}\text{C}$  records (Gagan et al., 1996).

### Minor and trace elements

Studies of trace elements in corals have generally focused on elements that substitute for calcium in the aragonite crystal lattice, and the amount of trace element is usually expressed as an element/Ca ratio. The most studied elements in coral aragonite are divalent cations that are abundant in seawater (i.e., Mg, Sr, U, Ba, and B) and have chemical properties similar to calcium. Less-abundant divalent cations occur in trace abundances ( $<1$  nmol/mol Ca – 1  $\mu\text{mol/mol}$  Ca) in corals. In some cases, trace elements may be adsorbed on the coral skeletal surface or concentrated in occluded organic matter. Therefore, in general thorough cleaning of coral samples is required to remove trace elements that are not incorporated into the aragonite lattice to avoid artifacts in environmental reconstructions (e.g., Shen et al., 1987; Fallon et al., 1999).

Many of the trace element proxies discussed below are still being developed and the systematics of their incorporation in coral aragonite requires further testing before they can be considered robust indicators of environmental conditions. The following section summarizes the most common trace elements studied in corals, broadly separated under three headings on the topics of paleothermometry, ocean–atmosphere–land interactions, and human impacts on the marine environment.

### Paleothermometry

Trace elements in coral skeletons are most commonly used as a proxy for ocean temperature. Strontium/calcium (Sr/Ca) in coral aragonite is the most established and reliable paleothermometer. Early studies indicated that there was a small inverse relationship ( $\sim 1\%$  decrease in Sr/Ca per  $^{\circ}\text{C}$ ) between SST and coral Sr/Ca (Weber, 1973; Smith et al., 1979). In a breakthrough study, Beck et al. (1992) used precise isotope dilution thermal ionization mass spectrometry to establish a  $0.6\%$  decrease in Sr/Ca per  $^{\circ}\text{C}$  with analytical precision equating to  $\pm 0.05^{\circ}\text{C}$ . Since then, coral Sr/Ca–SST calibrations have been developed for a wide range of reef sites around the Pacific and Indian Oceans (e.g., McCulloch et al., 1994; Shen et al., 1996; Alibert and McCulloch, 1997; Gagan et al., 1998; Marshall and McCulloch, 2002). A review of 38 published Sr/Ca–SST relationships for *Porites* corals found that the mean Sr/Ca–SST dependence is  $0.061$  mmol/mol per  $^{\circ}\text{C}$  (Corrège, 2006).

A primary assumption in coral Sr/Ca paleothermometry is that biological effects on coral Sr/Ca are negligible, leaving SST as the primary factor controlling Sr uptake. While coral growth rate and algal symbiont photosynthesis have a marked influence on coral Sr/Ca (e.g., Cohen et al., 2001), it has been shown that biological effects are usually only significant at low coral growth rates, or where geochemical sampling is not made along a major coral growth axis (de Villiers et al., 1994; de Villiers et al., 1995; Alibert and McCulloch, 1997; Gagan et al., 1998; Mitsuguchi et al., 2003). Nevertheless, there are, in some cases, significant differences between the intercepts of individual Sr/Ca–SST calibration equations and the source of these offsets is yet to be fully understood. Some of the offsets may be explained by slight differences in seawater Sr/Ca between different regions (de Villiers, 1999), or by differences between the temperature of the coral microenvironment and the SST records used to calibrate coral Sr/Ca. It has also been suggested that the influence of light levels on coral calcification and Sr uptake (Cohen et al., 2001) could explain some differences in coral Sr/Ca–SST calibrations (Gagan et al., 2004). As for coral  $\delta^{18}\text{O}$ , the potential for Sr/Ca offsets between coral colonies means that reliable records of mean SST can only be derived using a large number of corals of similar age (e.g., Hendy et al., 2002; Abram et al., 2009).

The other fundamental assumption used in coral Sr/Ca thermometry is that the Sr/Ca composition of seawater has remained constant through time. Given the long oceanic residence time of Sr (2.5 million years) and Ca (0.6–1.1 million years), this assumption was thought to be valid over glacial-interglacial timescales. However, it has been proposed that the concentration of Sr in seawater may increase during glacial episodes due to weathering of shelf carbonates during sea-level lowstands (Stoll and Schrag, 1998). This sea-level-related effect has the potential to produce cool artifacts of up to  $1.5^{\circ}\text{C}$  in fossil coral Sr/Ca records. Also, it has been shown that Sr/Ca in



surface seawater is greater where intense upwelling brings Sr-enriched water to the surface. Again, not accounting for this process can result in overestimation of SST cooling from coral Sr/Ca records (de Villiers, 1999).

To date, Sr/Ca in modern and fossil corals preserved in submerged and tectonically raised reefs has been used to great effect to document the sensitivity of tropical climate to changing boundary conditions throughout the late Quaternary (see *Paleoclimate from Corals*). In addition to Sr/Ca, precise measurements of uranium/calcium (U/Ca) and magnesium/calcium (Mg/Ca) in corals have provided useful paleothermometers (Min et al., 1995; Shen and Dunbar, 1995; Mitsuguchi et al., 1996). The improved sensitivity of inductively coupled plasma mass spectrometry has led to an increase in the speed and range of trace elements (e.g., B/Ca) that can be measured to examine thermal variations in the tropics (e.g., Sinclair et al., 1998; Fallon et al., 1999; Hendy et al., 2002). The U/Ca, Mg/Ca, and B/Ca SST proxies show higher variability between sites and corals, and so are generally considered less reliable for SST reconstructions than Sr/Ca (Fallon et al., 2003). They are, however, useful additional tracers for verifying SST changes identified by coral Sr/Ca.

## Ocean–atmosphere–land interactions

### *Ultraviolet luminescence*

Luminescent banding, also known as fluorescent banding, can be observed in *Porites* corals from areas that are influenced by river runoff, and was first described by Isdale (1984). Luminescence in coral aragonite occurs under ultraviolet light and is caused by marine fulvic acids (“blue” under ultraviolet light) and terrestrial fulvic and humic acids (“yellow-green”) of relatively low molecular mass in the coral skeleton. These compounds are often seen as distinct bands in corals and it is hypothesized that increased luminescence marks the influx of fulvic acids into seawater during terrestrial runoff events (Boto and Isdale, 1985). An alternate theory is that luminescent bands are the result of reduced coral calcification in response to the low salinity produced by runoff events (Barnes and Taylor, 2001).

The use of coral luminescent banding to reconstruct river runoff has been particularly successful in the Great Barrier Reef, Australia, where Isdale (1984) found a good correspondence between the timing, width, and intensity of luminescent bands in nearshore corals and historical flood events of the Burdekin River. Lough (1991) demonstrated the statistical validity of the luminescence record for reconstructing past rainfall variations over much of northeast Australia. The Great Barrier Reef coral luminescence record has since been developed as a chronological tool for cross-dating between corals (Hendy et al., 2003) and as a proxy for ENSO-related variability of river flow (Lough, 2007). Beyond the Great Barrier Reef, the development of quantitative transfer functions relating luminescent banding to climatic parameters has been hindered by lack of knowledge about the

production rates and exact sources of humic and fulvic acids, as well as the mechanism (i.e., passive or active) for their uptake into the coral skeleton. However, a study of luminescence in last interglacial fossil corals from the Red Sea showed that fluorescence can persist for tens of thousands of years, and suggests that runoff to the Red Sea was greater during the last interglacial (Klein et al., 1990).

### *Barium and cadmium*

Barium/calcium (Ba/Ca) appears to be a conservative tracer that is incorporated into coral aragonite in proportion to its concentration in ambient seawater. Changes in the Ba content of seawater can be related to the upwelling of nutrient-rich (Ba-rich) subsurface water. Given that Ba has a nutrient-like distribution in the water column, Ba/Ca in corals from outer barrier reef locations or upwelling zones has been shown to reflect the intensity of ocean upwelling (Lea et al., 1989). Similarly, coral Cd/Ca has been proposed as a proxy for upwelling intensity and productivity (Shen et al., 1987). However, despite early studies demonstrating a link between ocean upwelling and coral Ba/Ca and Cd/Ca ratios, the practical application of these tracers has been somewhat limited (Reuer et al., 2003; Montaggioni et al., 2006; Alibert and Kinsley, 2008). A recent assessment of coral Cd/Ca records using multiple corals from the Gulf of Panama suggests that several individual records are required to reliably reconstruct ocean upwelling (Matthews et al., 2008).

In nearshore reef settings of the Great Barrier Reef and Kenya, coral Ba/Ca records have been interpreted as proxies for riverine sediment flux (McCulloch et al., 2003; Fleitmann et al., 2007). The coincidence of Ba/Ca peaks with luminescent bands in these nearshore coral records is used as evidence that the Ba is derived from sediments incorporated in river flow. Both records document dramatic increases in soil erosion related to European settlement and changes in land usage. Also, it has been shown that Great Barrier Reef runoff influences the concentration of manganese and rare earth elements in nearshore seawater, and that the combined use of these elements with Ba/Ca can enhance the interpretation of changes in riverine sediment flux (Wyndham et al., 2004; Lewis et al., 2007).

### *Manganese and rare earth elements*

Manganese (Mn) and rare earth elements (REEs) are incorporated into coral skeletons in close proportion to their concentrations in seawater and are potentially useful proxies for biological activity and redox conditions in the water column (Shen et al., 1991; Sholkovitz and Shen, 1995; Wyndham et al., 2004). Seasonal cycles can be observed in the concentration of Mn and REEs in coral skeletons, and in the relative proportion of light to heavy REEs. It has been proposed that this cyclicity reflects a seasonal control on the dissolution of Mn-oxide particles (and associated adsorbed REEs). The dissolution of Mn-oxide may be caused by insolation-driven increases in photoreduction in spring and/or by reducing conditions

resulting from the decay of organic matter produced by spring algal blooms (Alibert et al., 2003; Fallon et al., 2003). At Tarawa atoll, in the central equatorial Pacific, increases in coral Mn during El Niño events have been attributed to wind-driven sediment resuspension allowing Mn to be released to the water column (Shen et al., 1992). Distinct increases in coral Mn and REEs have also been used as evidence for anoxic conditions that resulted in widespread reef death following a large red-tide algal bloom in Indonesia (Abram et al., 2003).

## Human impacts on the marine environment

### *Radiocarbon and nuclear weapons testing*

Nuclear weapons testing in the 1950s produced excess radiocarbon ( $^{14}\text{C}$ ) in the atmosphere, and the oceanic uptake of some of this  $^{14}\text{C}$  has increased the contrast between surface and deep ocean  $^{14}\text{C}$  concentrations.  $^{14}\text{C}$  in coral aragonite tracks  $^{14}\text{C}$  concentrations in the dissolved inorganic carbon of surface seawater. The increase in bomb-produced  $^{14}\text{C}$  in the surface ocean was first measured in *Diploria* and *Montastrea* corals from the Atlantic (Druffel and Linnick, 1978; Nozaki et al., 1978). Since then, several studies have documented differences in the timing and amplitude of the  $^{14}\text{C}$  “bomb-spike” in coral records to study air–sea exchange processes, the mixing of bomb  $^{14}\text{CO}_2$  between the surface mixed layer and upper ocean, and ocean circulation in the tropics (e.g., Druffel, 1987; Toggweiler et al., 1991; Brown et al., 1993; Moore, 1997; Guilderson et al., 1998; Grunet et al., 2004). Coral  $^{14}\text{C}$  records play an important role in providing boundary constraints used to test the parameterization of ocean dynamics in ocean circulation models (e.g., Rodgers et al., 1997).

The oceanic signature of the relatively small reduction of  $^{14}\text{C}/^{12}\text{C}$  in atmospheric  $\text{CO}_2$  produced by the Suess effect has been much more difficult to discern in coral records. The Suess effect is due mainly to the input of  $^{14}\text{C}$ -free  $\text{CO}_2$  from fossil fuel burning into the atmosphere and ocean since ~AD 1850. Variations in surface-ocean  $^{14}\text{C}/^{12}\text{C}$  on century-decade time scales mask the Suess effect in coral records, but provide information on vertical mixing, ocean circulation, and redistribution of surface-waters associated with ENSO (e.g., Toggweiler et al., 1991; Druffel and Griffin, 1993; Guilderson and Schrag, 1998).

### *Lead, cadmium, and industrial pollution*

Lead (Pb) and cadmium (Cd) in coral skeletons record local and global inputs of industrial heavy metal pollution to the oceans (e.g., Shen and Boyle, 1987; Shen et al., 1987; Shen and Boyle, 1988). An important study by this group measured Pb/Ca and Cd/Ca in a Bermuda coral to show that atmospheric fluxes of industrial pollution reached the western North Atlantic from the continental USA via the westerlies. Peaks in Pb/Ca in the coral correlated with the use of tetraethyl lead in automobile gasoline. The initial rise in Cd from 1900 to 1925 was coincident with a rise in zinc production (from which Cd

is a byproduct) that occurred at a time when flue dust recovery was negligible. Similarly, measurements of Pb/Ca in corals from the western Pacific and adjacent seas showed a clear pattern of atmospheric Pb transport from the Asian continent to the open ocean since the late nineteenth century (Inoue et al., 2006).

### *Boron isotopes and seawater pH*

Reconstructing the recent trend and natural variability of ocean pH is crucial to understand the possible consequences of ocean acidification on marine ecosystems due to the absorption of anthropogenic  $\text{CO}_2$  by seawater. Culturing experiments on *Porites* and *Acropora* corals have confirmed that boron isotopes ( $\delta^{11}\text{B}$ ) in coral skeletons faithfully record variations in seawater pH (e.g., Hönisch et al., 2004; Reynaud et al., 2004). The calibration of  $\delta^{11}\text{B}$  with seawater pH for *Porites* is in good agreement with the theoretical curve for the borate species (Hönisch et al., 2004), the major form in which B is incorporated into coral skeletons. However, there is still uncertainty about how biological modulation of B uptake associated with coral calcification may influence paleo-pH records (Gaillardet and Allégre, 1995).

To date, two multi-century records of seawater pH from  $\delta^{11}\text{B}$  have been determined for *Porites* corals, one from Flinders Reef in the Coral Sea (Pelejero et al., 2005) and the other from the central Great Barrier Reef (Wei et al., 2009). The Flinders coral  $\delta^{11}\text{B}$  record, commencing in AD 1708, shows large variations in pH over ~50-year cycles that covary with the Interdecadal Pacific Oscillation. The results indicate that locally significant natural cycles in reef pH can modulate the impact of ocean acidification on coral reef ecosystems. The Great Barrier Reef coral  $\delta^{11}\text{B}$  record, spanning AD 1800–2004, shows an overall trend of ocean acidification with pH decreasing by 0.2–0.3 units since ~1940. The result suggests that increasing levels of atmospheric  $\text{CO}_2$  have already caused significant acidification of the ocean surface.

### *Phosphorous, nitrogen, trace elements, and reef pollution*

Phosphorous (P) and nitrogen isotopes ( $\delta^{15}\text{N}$ ) in corals have been used to reconstruct the history of sewage and agricultural pollution in nearshore reef settings. Phosphate acts as a crystal poison of calcification and Dodge et al. (1984) showed that concentrations of P in corals from the North Atlantic are consistent with the local sewage and pollution history. In principle, the  $\delta^{15}\text{N}$  of residual organic nitrogen in coral skeletons should reflect temporal changes in the balance between natural and anthropogenic nitrogen sources in coastal reef waters. Synthetic nitrogenous fertilizers are typically depleted in  $^{15}\text{N}$  relative to the inorganic nitrogen dissolved in seawater. This technique has been used to show that Western-style agricultural practices since 1970 have contributed to the degradation of coastal reefs in Bali, Indonesia (Marion et al., 2005).

Other trace metals in corals have been shown to be good tracers of pollutants in coral reef environments (e.g., Howard and Brown, 1987; Scott, 1990; Guzman and Jimenez,

1992; Guzman and Jarvis, 1996). A recent study showed that REE (Y, La, Ce), Zn, and Pb concentrations increased significantly in *Porites* corals from Misima Island, Papua New Guinea following the commencement of open-cut gold mining at Misima in 1989 (Fallon et al., 2002).

## Summary

The stable isotopic and trace element compositions of coral skeletons provide a wealth of information about past environmental conditions in reef settings. Interpretation of existing proxies continues to be refined, while the development of new proxies is shedding light on a range of environmental parameters. As the number of stable isotopic and trace element records grows, it is becoming increasingly important to view coral records in spatial networks to enhance the climatic interpretations that can be drawn from them. An important aspect of this involves archiving the geochemical data (and appropriate metadata) derived from corals. We refer readers to the NOAA Climatic Data Center Paleoclimatology website (<http://www.ncdc.noaa.gov/paleo/corals.html>), which is the premier data archive for scientists interested in understanding natural climate variability and future climate change.

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## Cross-references

[Aragonite](#)  
[Calcite](#)  
[Climate Change and Coral Reefs](#)  
[Cold-Water Coral Reefs](#)  
[Diagenesis](#)  
[Earthquakes and Emergence or Submergence of Coral Reefs](#)  
[El Niño, La Niña, and ENSO](#)  
[Emerged Reefs](#)  
[Nutrient Pollution/Eutrophication](#)  
[Ocean Acidification, Effects on Calcification](#)

[Paleoclimate from Corals](#)  
[Porites](#)  
[Radiocarbon \( \$^{14}\text{C}\$ \): Dating and Corals](#)  
[River Plumes and Coral Reefs](#)  
[Sclerochronology](#)  
[Submerged Reefs](#)  
[Upwelling and Coral Reefs](#)  
[Uranium Series Dating](#)

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## STEERS, JAMES ALFRED (1899 – 1987)

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(James) Alfred Steers (1899 – 1987), coastal physiographer and early promoter of coastal zone planning and coastal conservation. His entire academic career was spent in the Department of Geography, University of Cambridge, England, entering the Department as an



**Steers, James Alfred (1899 – 1987), Figure 1** Steers and surficial geomorphology of the Great Barrier Reef. The Second International Coral Reef Symposium, held in 1973, was a remarkable undertaking, involving steaming north from Brisbane to Lizard Island and back on a cruise liner, the MV Marco Polo. On board were two members of the 1928–1929 Expedition, Maurice Yonge and Alfred Steers. The meeting coincided with the Royal Society – Universities of Queensland Expedition to the northern Great Barrier Reef, led by David Stoddart. Here Alfred Steers (*far left*), Richard Orme (*second left*, 1973 Expedition member), David Stoddart (*back to camera*) and other symposium participants discuss the shingle rampart features at Low Isles (photograph: David Hopley).



undergraduate in 1916 and retiring as Professor of Geography in 1966. He was the senior member of the Geographical Section of the Great Barrier Reef Expedition to Low Isles 1928–1929, led by C. M. Yonge, where he was involved in regional survey and detailed island mapping of the “low wooded islands” of Low Isles and Three Isles with M. Spender. Fieldwork on the Reef led to early speculations on regional tectonics, sea-level change and reef island development and this was followed by a second expedition in 1936 when reef islands were extensively mapped between 24°S (Bunker and Capricorn Groups) and 13°S (Cape Direction). Steers subsequently encouraged reef mapping on the Great Barrier Reef using aerial photography and was a member of the planning committee that resulted in the Royal Society of London and Universities of Queensland Expedition to the northern Great Barrier Reef in 1973, led by D. R. Stoddart (Figure 1). In 1939, Steers participated in an expedition to Jamaica (leader: V. J. Chapman; mapping of Port Royal Cays, Morant Bank cays, Palisadoes spit) which was curtailed by the outbreak of World War II. In 1977, with Stoddart, he published two synthesis papers on the origin of fringing reefs, barrier reefs and atolls and on the typology and origin of reef islands.

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## Cross-references

[Great Barrier Reef Committee](#)  
[Low Wooded Islands](#)  
[Royal Society of London](#)  
[Stoddart, David Ross \(1937–\)](#)  
[Yonge, Sir Maurice \(1899–1986\)](#)

science and organizer of international reef science from the Department of Geography, University of Cambridge, England 1956–1988 (pupil of J.A. Steers; PhD on the Belize Barrier Reef, 1964); thereafter Professor of Geography, University of California at Berkeley. Significant contributions to the modern description and re-description of reef landforms in all the major reef provinces, characterized by careful field observations (including detailed surface mapping), use of the comparative method, and an ability to consider the interplay of the different time and spatial scales of controlling processes, including an appreciation of environmental variability and the role of extreme events. Stoddart has made major contributions to the understanding of tectonics and sea level dynamics on Pleistocene, Holocene, and historical time scales and their implications for coral reef geomorphology and ecology; to ocean basin biogeography; to coral island floristics and ecology; and to the history of coral reef science. He has also made notable contributions to coral reef conservation, most particularly in the saving of Aldabra Atoll, S.W. Indian Ocean for science. He was the key energizer of the international coral reef symposia, a member of the Editorial Board of the Atoll Research Bulletin since 1969, a founding member and initiator of the International Society for Reef Studies, its first President, and subsequently coordinating editor of the journal ‘Coral Reefs’.

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[Belize Barrier and Atoll Reefs](#)  
[Great Barrier Reef Committee](#)  
[Royal Society of London](#)  
[Sea-level Indicators](#)  
[Steers, James Alfred \(1899–1987\)](#)  
[Yonge, Sir Maurice \(1899–1986\)](#)

## STODDART, DAVID ROSS (1937–)

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David Ross Stoddart (1937–) geomorphologist, Quaternary scientist, tropical botanist, historian of coral reef

## STROMATOLITES

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### Synonyms

Laminated microbialites (see Chapter *Microbialites*)

### Definition

Stromatolites are lithified laminated organosedimentary deposits produced by the sediment trapping, binding, and/or precipitation activities of microbial communities dominated by photosynthetic bacteria (modified from Awramik, 1992).

### Introduction

Stromatolites are Earth's earliest and most persistent reefs. They are conspicuous and widespread components of Precambrian carbonate platforms and are still forming in modern environments (Figure 1). Despite over a 100 years



**Stromatolites, Figure 1** Ancient and modern stromatolites. (a) Archean stromatolites on shallow platforms fringing volcanoes; painting by P. Sawyer, reprinted with permission from Natural History Museum, Smithsonian Institution. (b) Modern stromatolites on the margins of Hamelin Pool, Shark Bay, Western Australia.

of research, the significance, origin, and very definition of stromatolites are, however, still disputed (Semikhatov et al., 1979; Ginsburg, 1991; Grotzinger and Knoll, 1999; Riding, 1999; Awramik and Grey, 2005; Schopf, 2006).

Derived from the Greek “stroma,” meaning mattress or stratum, and “lithos,” meaning rock, the term stromatolite was introduced by Kalkowsky (1908) to refer to “organogenic, laminated calcareous rock structures, the origin of which is clearly related to microscopic life, which in itself must not be fossilized” (translated in Krumbein, 1983, p. 499). This definition requires that “microbial influence be interpretable from features of lamination and texture in the absence of direct paleontologic evidence for mat organisms” (Grotzinger and Knoll, 1999, p. 316). With such ambiguity, there is major disagreement as to whether the definition of stromatolite should be genetic or purely descriptive (see for example, Krumbein, 1983; Grotzinger and Knoll, 1999; Riding, 1999). An often used non-genetic definition is that a stromatolite is an “attached laminated lithified sedimentary growth structure, accretionary away from a point or limited surface of initiation” (Semikhatov et al., 1979). This purely descriptive definition allows for terms, such as “abiogenic stromatolite,” which, it could be argued, corrupt the original intent of the term (Awramik and Grey, 2005).

In this review, the term stromatolite is used in the traditional sense of Kalkowsky for lithified, laminated sedimentary structures formed as a result of microbe–sediment interactions. As such, stromatolites are a subset of microbialites, a term coined by Burne and Moore (1987) to include all organosedimentary deposits that have accreted as a result of benthic microbial communities trapping and binding sediment and/or forming the locus of mineral precipitation. Stromatolites are differentiated from other types of microbialites, such as thrombolites (with clotted textures), by their layered internal structure.

Dominating the fossil record for 80% of Earth history, stromatolites are potentially a major source of information on the early Biosphere (Awramik, 1992; Walter, 1994). Scientists believe, moreover, that the photosynthetic activity of cyanobacteria (formerly known as blue-green algae and commonly regarded as the most important group of stromatolite-forming microorganisms) generated the oxygen of our atmosphere (Schopf et al., 1983). An oxygen-rich atmosphere was critical to the development of higher forms of life on Earth.

Described at a variety of scales, stromatolites form ridges and bioherms composed of individual buildups with shapes ranging from simple domes to elaborately branched columns. Millimeter-scale lamination, visible with the naked eye, shows diverse microstructures when viewed in petrographic thin section. Variations in stromatolite structures, from megascale to microscale features, reflect the interaction of biological and geological activities on an evolving Earth.

## Stromatolites on early Earth

The fossil record of stromatolites spans more than three billion years, dating back to the Archean. Precambrian stromatolites constructed impressive reef complexes, rivaling any in later periods. Individual stromatolites are the “framebuilding” constituents of Precambrian reefs—analogs to the calcified metazoans of Phanerozoic reefs. The overall geometry and growth morphology of Precambrian reefs was a function of platform position and is similar to the distribution of metazoan reefs on Phanerozoic platforms. This illustrates the universal importance of bioherms in carbonate facies development, regardless of reef-building organisms (James and Geldsetzer, 1988; Aitken, 1988).

The first stromatolites occur in the Early Archean (3.8–3.3 billion years ago). Although the Early Archean was dominated by active tectonism and volcanism, small isolated carbonate platforms with stromatolites formed during brief quiescent periods. Despite reports questioning the biogenicity of Early Archean stromatolites (e.g., Lowe, 1994; Brasier et al., 2004), there is compelling evidence that these ancient structures are products of mat-building communities (Schopf, 2006; Awramik, 2006). Stromatolites in the Strelly Pool Chert in Western Australia, for example, are unusually well preserved and morphologically diverse (Allwood et al., 2006, 2007). These stromatolites formed in shallow marine environments with low rates of terrigenous sedimentation and no direct input from high temperature hydrothermal systems; the compositions and textures of the stromatolites are indicative of microbially influenced sedimentation (Allwood et al., 2006, 2007). The remarkable Strelly Pool Chert stromatolites thus provide “ecosystem-scale insights into early life on Earth” (Allwood et al., 2007, p. 198).

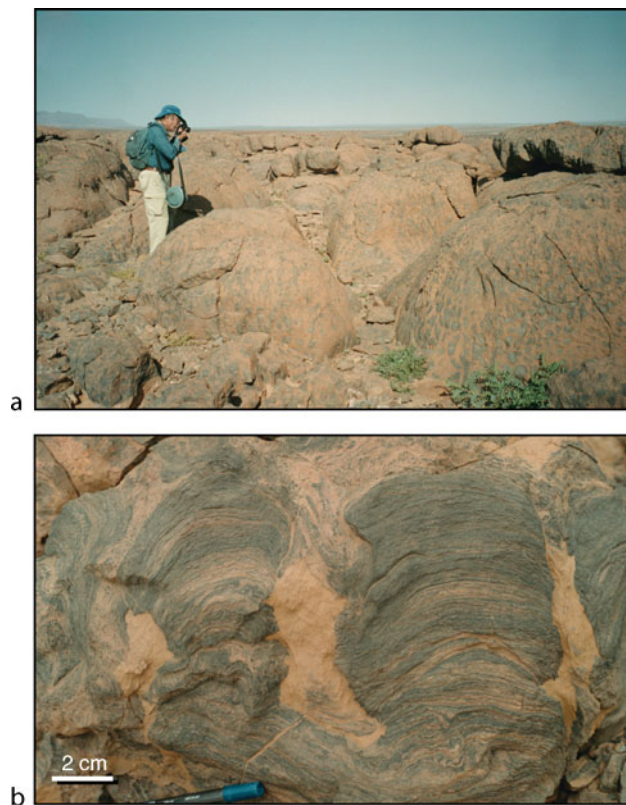
With the gradual development of stable continents during the Middle and Late Archean (3.3–2.5 billion years ago), carbonate platforms and stromatolites became increasingly common. One of the best known Late Archean examples is the stromatolite-rimmed Campbellrand carbonate belt of South Africa, which is more than 1.5 km thick (Grotzinger, 1994). Full development of large continents with spacious shallow water platforms allowed extensive development of stromatolite reef systems on a global-scale during the Proterozoic (2.5–0.5 billion years ago; Figure 2). Early Proterozoic stromatolite barrier reefs in Canada, for example, attained thicknesses of 1 km and lengths of 600 km (Hoffman, 1988; Hoffman and Grotzinger, 1988). During Early and Middle Proterozoic time, high energy reef margins were characterized by belts of strongly elongated stromatolitic mounds, with isolated domes in protected inner shelf environments and stromatolitic pinnacle reefs on deep water ramps.

The widespread occurrence of stromatolites on Precambrian platforms had major implications for carbonate budgets. Stromatolites were not only depositories, but were

also factories for carbonate production, with microbial activities inducing precipitation of carbonate within the stromatolitic mats, and/or in the water column above the stromatolites (Grotzinger, 1988). There were, moreover, notable changes in the style and mode of stromatolite accretion throughout the Precambrian, with precipitation dominating in Archean stromatolites, trapping and binding of micrite (fine grained carbonate,  $<4\ \mu\text{m}$ ) dominating in Late Proterozoic stromatolites, and both modes of accretion in the intervening periods (Grotzinger, 1994). To add to this complexity, inorganic seafloor precipitation was ubiquitous on Late Archean platforms, and may have formed layered domal structures that mimic stromatolites (Sumner and Grotzinger, 2000).

## Stromatolite decline

After reaching a peak in abundance and diversity during the Proterozoic, stromatolites subsequently declined. The exact timing of the decline remains a subject of debate, reflecting differing computational methods (Grotzinger and Knoll, 1999; Riding, 2006). The most recent estimates of the commencement of decline range from 1,250 to 700 million years ago (Walter et al., 1992; Awramik and



**Stromatolites, Figure 2** One billion year-old stromatolites in the Atar group, Mauritania, West Africa. (a) Meter-scale patch reefs. (b) Fine scale lamination in radiating columns of the stromatolite *Tungussia confusa*.



Sprinkle, 1999; Riding 2006). Reasons for the decline are similarly controversial, and include diversification and radiation of seaweeds capable of outcompeting microbial mats for space on the seafloor (Fischer, 1965; Monty 1973; Knoll and Swett, 1990; Grotzinger and Knoll, 1999), changes in seawater chemistry (Grotzinger, 1990; Fischer, 1965), and grazing, burrowing, and competition for space by metazoans (Awramik, 1971; Garrett, 1970; Walter and Heys, 1985).

Stromatolites show marked fluctuations throughout the Phanerozoic (Pratt, 1982; Riding, 2006). They are common features of Cambrian and Lower Ordovician platforms, although the first sessile metazoans began to share reef construction, with archeocyathids in Lower Cambrian reefs and corals and sponges in Lower Ordovician reefs. Stromatolites declined markedly with major diversification of reef-building metazoans in Middle Ordovician, although microbial buildups remained locally important (Pratt, 1982). Stromatolites showed a resurgence during the Late-Devonian–Early Mississippian, and again in the Early Triassic, giving rise to the concept that they are “disaster biotas” (Schubert and Bottjer, 1992), thriving in the aftermath of mass extinctions, when competition from eukaryotic plants and animals was greatly reduced. Stromatolites were generally scarce during the Cenozoic.

### Modern stromatolites

For years, living stromatolites were thought to be extinct. Then, in the 1960s, modern stromatolites were found in Shark Bay, Western Australia, where the seawater is too salty for most animals and plants to survive (Figure 1b; Logan, 1961; Playford and Cockbain, 1976). Since the Shark Bay discovery, stromatolites have been found in a wide variety of modern environments, including saline lakes in Australia (e.g., Lake Thetis and lakes on Rottnest Island; Reitner et al., 1996); hypersaline lakes on Bahamian islands (e.g., Storr’s Lake on San Salvador; Mann and Nelson, 1989; Neumann et al., 1988), a brackish water lagoon in Belize (Chetumal Bay, Rasmussen et al., 1993), fresh water lakes in Antarctica (Parker et al., 1981), alkaline lakes in Tonga (e.g., Caldera lakes of Niuafo’ou Island; Kazmierczak and Kempe, 2006), and continental or subaerial settings (e.g., Verrecchia et al., 1995). In these examples, local development of harsh environmental conditions excludes most eukaryotes and allows stromatolite-building microorganisms to become the dominant community.

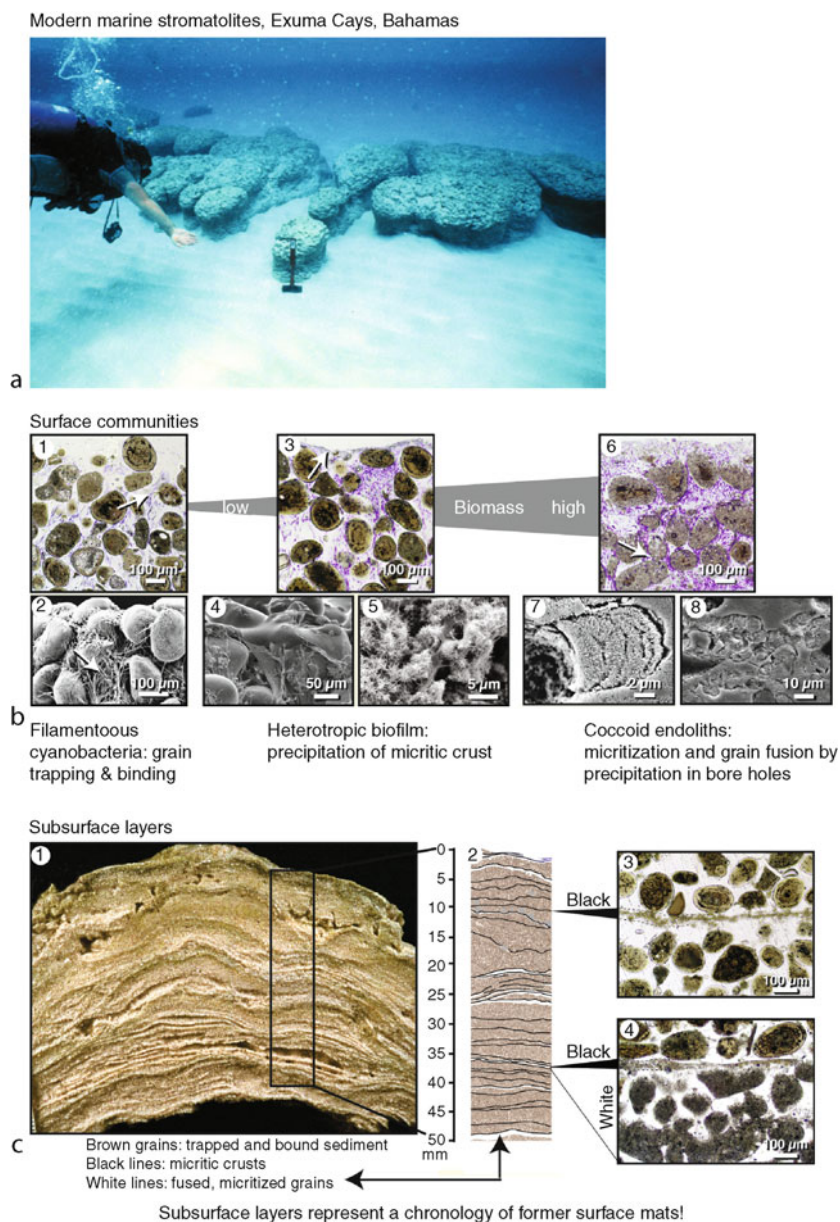
The first modern stromatolites growing in open marine conditions were discovered in Schooner Cays, Bahamas in the early 1980s (Dravis, 1983). Additional occurrences of open marine stromatolites have since been found at several additional localities along the margins of Exuma Sound, Bahamas, including Lee Stocking Is., Stocking Island, Highborne Cay, and Little Darby Island (Figure 3a) (Dill et al., 1986; Reid et al., 1995). As the only known examples of modern stromatolites forming in open marine environments similar to those of

Precambrian carbonate platforms, Exuma stromatolites have been a subject of intense investigation for the past decade (e.g., Stolz et al., 2009; Dupraz et al., 2009; Baumgartner et al., 2006, 2009; Decho et al., 2009; Foster et al., 2009; Desnues et al., 2008; Eckman et al., 2008; Visscher and Stolz 2005; Reid et al., 2000; Visscher et al., 2000; and additional publications listed at <http://www.stromatolites.info>). These studies serve as a basis for studying stromatolite morphogenesis and investigating factors leading to a dominance of microbes vs. metazoans as dominant reef builders (e.g., Reid et al., 2000; Andres and Reid, 2006; Andres et al., 2009).

Exuma stromatolites form as columns and ridges, ranging in height from several centimeters to 2 m. Millimeter-scale lamination in these stromatolites is visible in cut sections as alternations of hard and soft layers (Figure 3c; Reid et al., 1995). The soft layers, which are 1–2 mm thick, are composed primarily of unconsolidated fine-grained carbonate sand with average grain size of 125–250  $\mu\text{m}$ . There are two types of hard layers, which stand out in relief on the cut sections: (1) thin crusts of micrite, 20–50  $\mu\text{m}$  thick, and (2) cemented layers of fused carbonate sand grains, 1–2 mm thick.

A model for the formation of laminae in Exuma stromatolites was developed on the basis of integrated studies relating subsurface microstructure to microbial populations on the surfaces of the stromatolites (Reid et al., 2000). Three surface “mat types,” each characterized by a distinct community are recognized (Figure 3b): Type 1 mats are characterized by a filamentous cyanobacterial community; Type 2 mats are a biofilm community dominated by heterotrophic bacteria; and Type 3 mats are characterized by an abundance of endolithic coccoid cyanobacteria. Each surface community is associated with the accretion of a distinct type of mineral deposit (Figure 3c): Type 1 filamentous cyanobacterial mats accrete unconsolidated layers of trapped and bound sand grains; Type 2 biofilms precipitate micritic crusts (Visscher et al., 1998, 2000); and coccoid endoliths of the Type 3 mats form cemented layers of fused microbored (micritized) grains (Macintyre et al., 2000). Stromatolite lamination results from a cycling of the three surface mats, with each subsurface layer representing a community that was, at one time, at the stromatolite surface (Figure 3c). It is important to note that lamination in stromatolites is fundamentally different from lamination in microbial mats. Lamination in microbial mats results from community stratification due to gradients in light intensity, whereas lamination in stromatolites results from interactions of mats with depositing sediment and/or precipitating minerals (Grotzinger and Knoll, 1999, p. 324).

As a result of the sandy textures of marine Bahamian stromatolites, some authors have proposed that these coarse grained structures, as well as similar sandy stromatolites in Shark Bay, are not appropriate analogs for fossil stromatolites, which are typically composed of micrite (e.g., Awramik and Riding, 1988). It has further been proposed that the differences in grain size reflect an evolution



**Stromatolites, Figure 3** Modern marine stromatolites from Exuma Cays, Bahamas. (a) Underwater photograph of columnar stromatolites about 40 cm high, Little Darby Island (b) Surface communities. B<sub>1,2</sub> – Type 1 mats; filamentous cyanobacteria (arrows) bind carbonate sand grains. B<sub>3,4,5</sub> – Type 2 biofilm; a continuous sheet of exopolymer with abundant heterotrophs drapes the surface, aragonite needles (B<sub>5</sub>) precipitate in this biofilm. B<sub>6,7,8</sub> – Type 3 mats; a surface biofilm overlies filamentous cyanobacteria and endolith infested grains, which appear gray and are fused. Banded pattern of fibrous aragonite in bore holes (B<sub>7</sub>) indicates progressive infilling. Precipitation in tunnels that cross between grains leads to fusion (B<sub>8</sub>) (c) Subsurface layers. C<sub>1</sub> – vertical cut section shows mm-scale lamination resulting from an alternation of hard and soft layers. C<sub>2</sub> – low magnification thin section photomicrograph of boxed area in C<sub>1</sub> showing the distribution of lithified layers (black and white lines). C<sub>3</sub> – micritic crust, equivalent to the black lines in C<sub>2</sub>. C<sub>4</sub> – layer of microbored fused grains, equivalent to the white lines in C<sub>2</sub>, underlying a micritic crust. Modified from Reid et al. (2003).

of stromatolite-building communities, from Precambrian prokaryotic communities, which trap, bind, and precipitate micrite, to Cenozoic communities that include macro and microalgae, in particular diatoms, which accrete sand (Awramik and Riding, 1988; Riding, 2000). Detailed growth studies of Bahamian stromatolites show, however, that modern marine sandy stromatolites can be accreted by purely prokaryotic communities (Reid et al., 2000). Moreover, the ecological model developed for Bahamian stromatolites, in which lamination results from the cycling of prokaryotic communities on stromatolites surfaces, may be applicable to other modern and fossil stromatolites. Of particular interest is precipitation of micritic crusts by the Type 2 biofilm community, as these crusts resemble micritic crusts in fossil stromatolites.

Precipitation of calcium carbonate in stromatolites is commonly linked to photosynthesis, resulting from an increase in alkalinity triggered by the uptake of  $\text{CO}_2$  by cyanobacteria (Pentecost and Riding, 1986; Arp et al., 2001; Aloisi, 2008). Although autotrophic primary production by cyanobacteria is of key importance in stromatolite mats, producing sticky exopolymeric substances (EPS), other microbial groups can play key roles in increasing carbonate saturation (Visscher and Stolz, 2005; Dupraz and Visscher, 2005; Dupraz et al., 2009). Indeed, micrometer-scale mapping of microbial activities in Exuma stromatolites shows correlations between carbonate precipitation in Type 2 biofilms and high rates of sulfate-reduction (Visscher et al., 1998, 2000). Precipitation of micritic crusts in these biofilms is attributed to an increase in alkalinity resulting from sulfate reduction and  $\text{Ca}^{2+}$  release from degraded EPS (Visscher et al., 1998, 2000; Reid et al., 2000). The result is precipitation of a thin crust of aragonite with an isotopic signature that confirms the role of sulfate reducing bacteria (Andres et al., 2006). Various microbial metabolisms driving the “alkalinity engine,” together with the exopolymeric matrix, are recognized as fundamental controls of carbonate precipitation in microbial mats (Dupraz et al., 2009).

Finally, living stromatolites in the back reef lagoons of coralline algal fringing reef complexes at Stocking Island and Highborne Cay, Bahamas, provide insight into controls governing the spatial distribution of microbial vs. metazoan reef builders in a modern setting (Andres et al., 2009). The reefs systems at Stocking Island and Highborne Cay have comparable histories. The microbial buildups are relatively recent additions to these reefs, with growth initiating 1,500–1,000 years ago (Macintyre et al., 1996; Andres et al., 2009). The distribution of metazoans (corals and coralline algae) vs. microbial components in the reefs is controlled by intensity and frequency of sediment stress, sand abrasion, and burial of reef biota (Steneck et al., 1998). Although the metazoans can stand some sediment stress, they cannot cope with extended periods of burial (Steneck et al., 1998). In contrast, cyanobacterial mats are largely unaffected by burial (Kromkamp et al., 2007; Perkins et al., 2007). Increasing sediment stress in the back reef lagoon of a coralline algae

ridge led to the demise of metazoans and prolific growth of stromatolites. The study of these modern analogs provides a process-oriented understanding of microbial reef development in time and space, which can be applied to the rock record (Andres et al., 2009).

## Summary

Stromatolites form an unusual and special type of reef. Unlike modern coral reefs, stromatolites are formed by microorganisms. These microorganisms trap and bind sand grains together and/or precipitate calcium carbonate to form laminated mounds of limestone. The layered internal structure of these reefs is a characteristic feature and the name “stromatolite” in Greek means “layered rock.”

Stromatolites dominated the planet for 80% of Earth history, forming massive reef complexes comparable to any built by corals or other frame-building organisms. The golden age of stromatolite growth was 2.5–1 billion years ago, during Early and Middle Proterozoic. Suffering a major decline with the appearance of eukaryotic plants and animals in the Late Proterozoic, stromatolites were confined to harsh environments lacking eukaryotes for much of the Phanerozoic.

Living stromatolites were unknown until the 1960s when they were discovered in Shark Bay, a hypersaline lagoon in Western Australia. They have since been found in numerous modern environments including saline, fresh water, and brackish settings. The only known examples of stromatolites forming in open marine environments similar to those of Precambrian platforms are on the margins of Exuma Sound, Bahamas. Exuma stromatolites are ideal model systems for studies of stromatolite morphogenesis. Lamination in these stromatolites results from a cycling of prokaryotic surface communities, with each layer in the subsurface “fossil” part of the stromatolite representing a former surface mat. Lithification of surface mats is syndepositional, and microbially induced. Exuma stromatolites are less than 1,500 years old; they thrive in locations where sediment stress restricts the growth of coral, macroalgae, and other reef-building eukaryotes. Studies of living stromatolites provide models for biogeochemical cycling, population dynamics, and mineral formation in the three billion year old microbial reef ecosystem.

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## Cross-references

Algae, Coralline  
Algae-Macro  
Bahamas  
Devonian Reef Complexes of the Canning Basin  
General Evolution of Carbonate Reefs  
Micrite

## SUBMARINE GROUNDWATER DISCHARGE

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### Synonyms

Groundwater inflow; Groundwater seepage; Submarine springs

### Definition

Submarine groundwater discharge (SGD) is the direct discharge of groundwater across the sediment–water interface into estuaries, bays, and the ocean. SGD occurs “wherever an aquifer is hydraulically connected with the sea through permeable sediments” (Johannes, 1980). In addition to fresh, terrestrially derived groundwater discharge, SGD also includes the recirculation of seawater through seafloor sediments (Burnett et al., 2006).

On some coastlines, SGD is an important natural source of nutrients for coral reefs (Johannes, 1980; Paytan et al., 2006) and other coastal ecosystems. In coastal regions, with high anthropogenic nutrient loadings in groundwater, even a small net flux of submarine groundwater can deliver a comparatively large flux of nutrients to the sea (Burnett et al., 2006).

Terrestrially derived SGD can enter the ocean as slow seepage, discharging from sedimentary aquifers, and more rapidly from springs, rock fractures, or karst galleries. Generally, terrestrially derived SGD is confined to the nearshore zone, usually to waters less than 10 m deep, but some evidence exists for further offshore groundwater discharge, e.g., from “Wonky Holes” in the Great Barrier Reef (Stieglitz, 2005). Globally, the total discharge of fresh groundwater to the ocean is estimated at less than 10% of the surface input from rivers into the ocean (Gallardo and Marui, 2006).

SGD fluxes can be measured either directly with seepage meters (vented benthic chambers), or indirectly by their footprint on the physicochemical characteristics of the overlying water column, e.g., by temperature or salinity depth profiles, or by natural and introduced tracers (Burnett et al., 2006). Natural radioactive tracers such as radon and radium isotopes are enriched in groundwater, and are used to investigate larger-scale water exchange. In addition, hydrological methods such as water-balance approaches and numerical modeling are commonly applied to evaluate catchment-scale estimates of SGD.

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### Cross-references

[Coral Cays-Geohydrology](#)  
[Great Barrier Reef Committee](#)  
[Nutrient Pollution/Eutrophication](#)

## SUBMARINE LITHIFICATION

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### Synonyms

Submarine Cementation

### Definition

Submarine lithification is a process by which coral-reef structures and associated sediments are lithified in their marine setting by the precipitation of submarine cements.

### Introduction

Little was known about this process of submarine lithification in modern coral reefs until the 1960s when first reports of submarine lithification were published from reefs off Barbados (Macintyre, 1967; Macintyre et al., 1968) and off Bermuda (Ginsburg et al., 1967). This was shortly followed by the 1969 Bermuda Conference on Carbonate Cements that brought together a major gathering of carbonate geologists to describe a variety of carbonate cements from both modern and fossil deposits with a focus on submarine lithification in modern coral reefs (Bricker et al., 1969). Subsequently, the phenomenon was more widely documented, notably in the reefs off Jamaica (Land and Goreau, 1970; Land and Moore, 1980), Bermuda (Ginsburg et al., 1971a, 1971b; Shinn, 1971; Ginsburg and Schroeder, 1973; Schroeder, 1972a, b; Schroeder and Zankl, 1974; Focke and Gebelein, 1978), the Red Sea (Friedman et al., 1974; Gvirtzman and Friedman, 1977; Brachert and Dullo, 1991), Belize (James et al., 1976; Shinn et al., 1982; Macintyre, 1984), the Caribbean coast of Panama



(Macintyre and Glynn, 1976; Macintyre, 1977, 1983), the Great Barrier Reef (Marshall and Davies, 1981; Marshall, 1983, 1986), Antigua (Macintyre et al., 1985), Florida (Lighty, 1985), and the Bahamas (Macintyre et al., 1996).

### Environmental conditions that promote submarine lithification

Two environmental conditions that appear to affect the degree of submarine lithification in coral reefs are (a) the period of time that a reef surface is exposed, which can be as much as 1,000–2,000 years for extensive lithification (Macintyre et al., 1968; Macintyre and Glynn, 1976; Macintyre, 1984), and (b) the amount of wave energy expended on a section of the reef. That is why reef zones having slow accumulation rates or subjected to high wave energy are extensively lithified, as is the case in the slowly accreting deeper fore-reef slopes of Belize (James and Ginsburg, 1979), Jamaica (Land and Moore, 1980), and the Red Sea (Brachert and Dullo, 1991) and in the wave-exposed seaward margins of the Great Barrier Reef (Marshall, 1986) and the algal reefs on the outer edge of the Bermuda platform (Shinn, 1971; Ginsburg et al. 1971a; Ginsburg and Schroeder, 1973). From a detailed study of submarine lithification in a fringing reef off Panama, Macintyre (1977) concluded that lithification is controlled by “the length of time that a section of the reef is exposed to near-surface conditions suitable for the precipitation of submarine cements” (p. 514).

Despite the assumed influence of wave energy, extensive submarine lithification can occur even in quiet lagoonal settings, as illustrated by the lithification found on the long-exposed ceiling of a submarine cave in the Belize lagoon (Macintyre, 1984) and exposed the areas of the Great Barrier Reef patch reefs such as One Tree Reef and Myrmidon Reef (Marshall, 1985, 1986). Although not yet lithified, micritic Mg-calcite has also been found precipitating in Belizean and Panamanian lagoonal sediments (Macintyre and Aronson, 2006).

### Composition of submarine cements

The cement found in modern coral reefs consists mainly of micritic Mg-calcite, along with minor amounts of aragonite (Macintyre and Marshall, 1988), although aragonite is more abundant in deeper outer slopes of reefs where large spectacular fans of “botryoidal aragonite” have been reported in Belize (Ginsburg and James, 1976, p. 431; James and Ginsburg, 1979, p. 117) and the Red Sea (Brachert and Dullo, 1991, p. 359).

The Mg-calcite cements characteristically consist of 14–19 mol%  $\text{MgCO}_3$ , ranging from 15 to 17% for Bermuda (Ginsburg and Schroeder, 1973), 18.5% for Jamaica (Land and Goreau, 1970), 16.6–18.8% for Panama (Macintyre, 1977), 14.5–16.3% for Belize (Macintyre, 1984), and 15.1–18.5% for Antigua (Macintyre et al., 1985). The strontium values of the aragonite cements are also fairly consistent: 8,120–8,460 ppm (Ginsburg and

James, 1976) and  $6,900 \pm 800$  ppm (Macintyre, 1984) for Belize;  $9,500 \pm 600$  ppm for Panama (Macintyre, 1977); 10,500 ppm for Jamaica (Land and Moore, 1980); and  $7,377 \pm 783$  to  $7,549 \pm 973$  ppm for Antigua (Macintyre et al., 1985).

Stable isotope values for Mg-calcite are consistent as well:  $+3.0\% \pm 1.0$   $\delta^{13}\text{C}$  and  $-0.5\% \pm 1.0$   $\delta^{18}\text{O}$  for Jamaica (Land and Goreau, 1970),  $+3.0$  to  $3.8\%$   $\delta^{13}\text{C}$  and  $0.0$  to  $+0.5\%$   $\delta^{18}\text{O}$  for dense Mg calcite from Belize, and  $+3.1$  to  $+3.5\%$   $\delta^{13}\text{C}$  and  $-1.1$  to  $-0.3\%$   $\delta^{18}\text{O}$  for Belizean microsugrosic Mg-calcite (Macintyre, 1984). Aragonite cements from the deep fore reef of Belize have yielded values of  $+3.3$  to  $+4.3\%$   $\delta^{13}\text{C}$  and  $+0.4$  to  $1.1\%$   $\delta^{18}\text{O}$  (James and Ginsburg, 1979).

### Textural characteristics of lithified reef frameworks

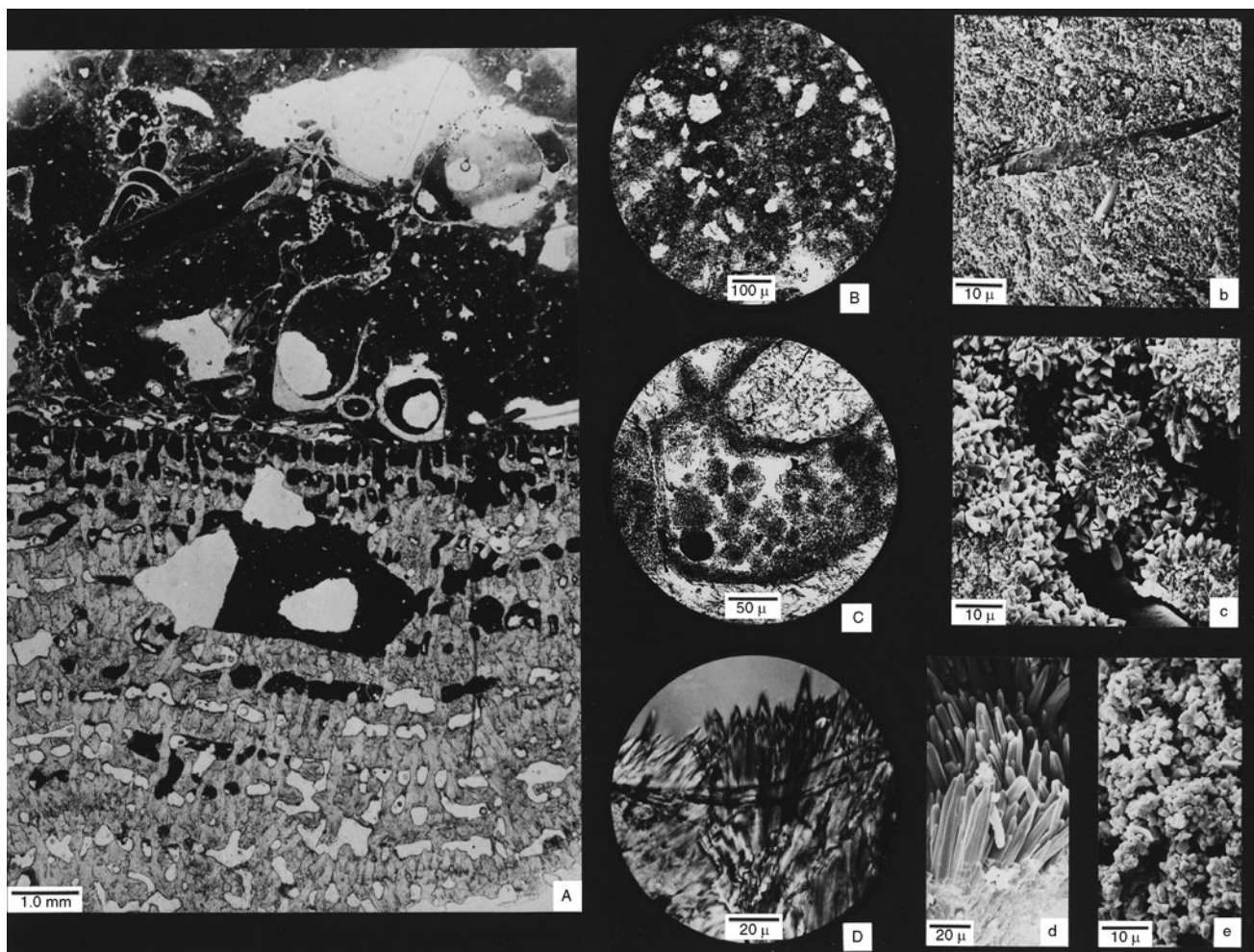
Lithified reef frameworks occur in two predominant forms, classified as micritic crusts and pavement limestones on the basis of their textures.

#### Lithified micritic crusts

The most common lithified reef texture consists of micritic Mg-calcite and varying amounts of sediment grains forming a crust on the upper surfaces of the coral framework (Figure 1). Crusts can be as much as 5 cm thick and cover any biota present on the surface, such as crustose coralline algae, bryozoans, foraminifera, serpulids, vermetids, and sabellarian tubes (Macintyre, 1977). In addition micritic Mg-calcite free of sediment grains penetrates up to 2 cm into coral skeletal cavities (Macintyre, 1977).

Petrographic studies reveal several distinct zones within the crust (Figure 1): sediment-rich micrite at the outer edge, grading into dense micrite, then a (20–60  $\mu\text{m}$ ) peloidal filling consisting of dense anhedral microcrystalline centers ( $>4$   $\mu\text{m}$ ) with microcrystalline (4–30  $\mu\text{m}$ ) well-developed dentate rims (Macintyre, 1985), and finally a porous submicrosugrosic ( $>4$   $\mu\text{m}$ ) Mg-calcite. At this inner limit, the coral skeletal sclerodermites have syntaxial overgrowths of acicular aragonite (Figure 1). This aragonite predates the Mg-calcite and rarely occurs in the same skeletal cavities (Macintyre, 1977).

Many of the thicker lithified crusts show distinct laminations described as “concentric laminations” (Land and Goreau, 1970, p. 406) and considered to be bedding surfaces. Some crusts contain inclined and overlapping bands (Figure 2), thought to indicate a “change in the slope of the accreting surface” (Macintyre, 1977, p. 507). Similar banding, described as “laminated mudstone in the form of irregular to superimposed domes” (James and Ginsburg, 1979, p. 135) has been found in the extensive lithified deposits of the deep fore reef off Belize, while “laminated micritic crusts” have been documented in the deep fore reef of the Red Sea (Brachert and Dullo, 1991, p. 361). Similar laminated crusts are also present in most major reef facies of One Tree Reef in the Great Barrier reef (Marshall, 1983).



**Submarine Lithification, Figure 1** Photomicrographs and scanning electron micrographs of the cement zonation pattern at the outer edge of a coral from Galeta reef, Panama. (A) Overall view of the cemented crust/infill zone at the outer edge of *Acropora palmata*. (Bb) Sandsize and finer sediment grains in a dense submicrocrystalline Mg-calcite mosaic in the outer crust. (Cc) Peloidal Mg-calcite infill of skeletal cavities at the outer edge of the coral. Note sparry dentate rim of microcrystalline Mg-calcite around submicrocrystalline peloids. (Dd) Acicular aragonite forming syntaxial overgrowths on coral skeleton spherulitic clusters. (e) Submicrocrystalline Mg-calcite at the innermost limit of Mg-calcite precipitation (Macintyre, 1977).

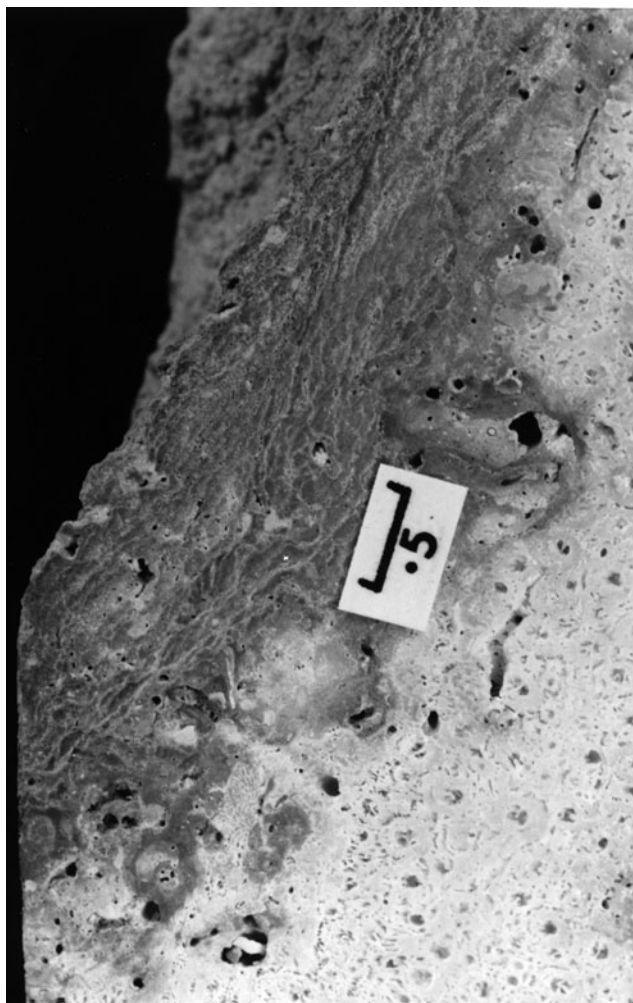
### Pavement limestones

The densest type of lithified reef structure occurs in areas where reef accumulation has experienced a hiatus and wave action is heavy, usually in the shallow fore reef or the outer edge of the reef flat, as found in Samoa (Carey, 1931), Enewetak (Ladd, 1973; Henny et al., 1974; Tracey and Ladd, 1974), Jamaica (Goreau, 1959), Belize (James et al., 1976; Rutzler and Macintyre, 1982), Panama (Macintyre, 1977), and the Great Barrier Reef (Marshall and Davies, 1981; Marshall, 1983). The sea floor may be extensively lithified even in parts of the deep fore reef where slopes are too steep for active reef accumulation, as in the Eastern Caribbean (Macintyre, 1972), Belize (James and Ginsburg, 1979), Jamaica (Land and Moore, 1980), and the Red Sea (Brachert and Dullo, 1991).

Typically, these heavily lithified areas of the sea floor have been exposed to long periods of boring, subsequent sediment filling, and micritic precipitation, with the result that the original skeletal framework has in many instances been entirely replaced by sediment-rich micritic Mg-calcite (Figure 3). This pattern is well documented in the reefs of Bermuda (Ginsburg and Schroeder, 1973; Schroeder and Zankl, 1974), Belize (James et al., 1976; James and Ginsburg, 1979), Panama (Macintyre, 1977, 1983), Jamaica (Land and Moore, 1980), and the Red Sea (Brachert and Dullo, 1991).

Another common feature of pavement limestones is a buried irregular eroded surface with an amorphous medium brown to black coating (Figure 3). These "hiatal corrosion surfaces" (Macintyre and Marshall, 1988,





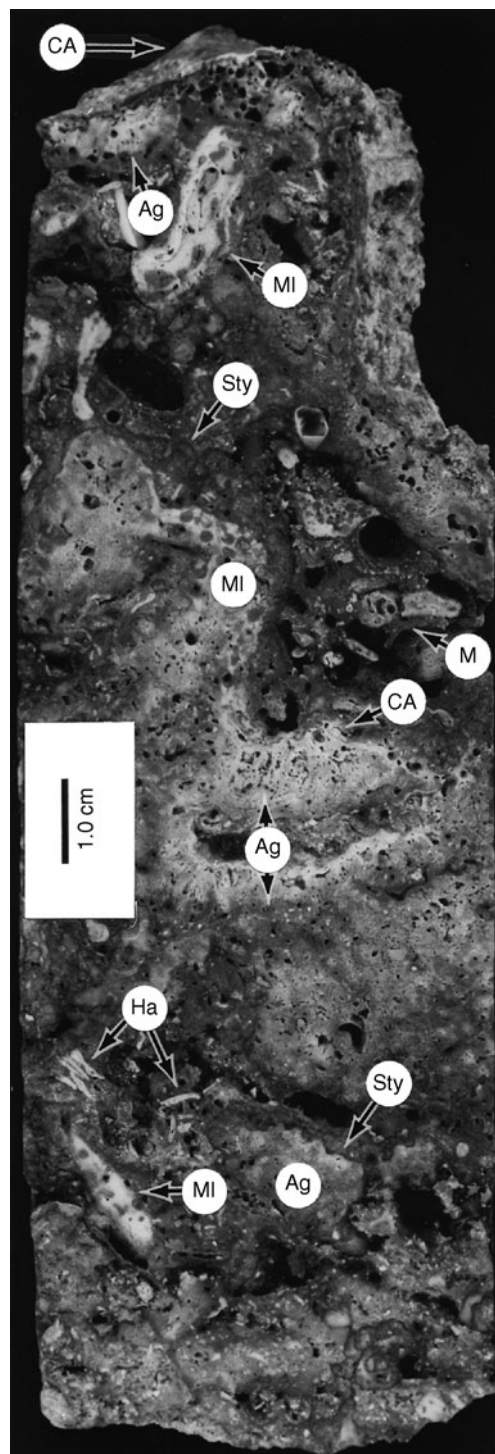
**Submarine Lithification, Figure 2** Inclined overlapping band in a micritic Mg-calcite crust on a Gelata reef, Panama coral (Macintyre, 1977).

p. 267) are said to resemble stylolitic structures in their irregularity, although “their lower surface is the only one truncating skeletal grains” (Macintyre, 1977, p. 510). Similar hiatal surfaces have been reported as “organic layers” in hard grounds in the Persian Gulf (Shinn, 1969, p. 124) and as dark coatings of iron and manganese oxides from the deep fore reef of Belize (James and Ginsburg, 1979) and Jamaica, where they are thought to represent “local inconformities or times of slow or bypassed sedimentation” (Land and Moore, 1980, p. 359).

### Origin of submarine lithification in coral reefs

The causes of submarine lithification in coral reefs are still not fully understood. Observations and experiments suggest that various organisms may play either a direct or indirect role in the precipitation of submarine cements.

Because well-lithified substrates occur in areas of heavy wave action, it has also been suggested that the pumping



**Submarine Lithification, Figure 3** Densely lithified pavement limestone showing multicyclic boring and infilling by sediment-rich micritic Mg-calcite that has almost totally replaced the original skeletal framework. Remnants of *Agaricia agaricites* (Ag), *Millepora complanata* (MI), and crustose coralline algae (CA) in a micritic Mg-calcite sediment-rich matrix includes *Halimeda* (Ha) and mollusc (M) grains. Note the stylolitic-like (Sty) dark hiatal corrosion surfaces (Macintyre, 1977).



action of waves (Mathews, 1974), as well as a reduction of  $\text{CO}_2$  due to pressure changes associated with heavy wave activity (Ginsburg et al., 1971b), may promote carbonate precipitation. The effect of wave-pumping activity may also be supplemented by supersaturation and low rates of accumulation (Focke and Gebelein, 1978).

Nonetheless, biological factors may play a more important role, as suggested by  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  enrichment in micritic crusts caused by organic-induced fractionation when crusts were formed (Land and Goreau, 1970). Further evidence of this role comes from the fatty acids present in micritic crusts, which are similar to the straight-chain 16-carbon acid formed by bacterial activity. "Micritic tubes" documented on the surface of some micritic crusts and thought to represent "filamentous algae, bacteria or fungi" (Brachert and Dullo, 1991, p. 357) provide additional support for a biological inducement in the precipitation of micrite. However, bacteria and fungi may have a more indirect effect, as indicated by laboratory experiments (Towe and Malone, 1970) in which the precipitation of both aragonite and Mg-calcite was observed following the release of ammonium carbonate in seawater (Figure 4). It was concluded "because ammonium carbonate can be a natural by-product of biological activity this suggests a mechanism by which such mineral phases might occur locally in marine conditions" (Towe and Malone, 1970, p. 348). This hypothesis was strongly supported by observations of major deposits of Mg-calcite coating serpulid tubes on the ceiling of a cave in the lagoon of the Belizean Barrier reef (Macintyre, 1984). Submarine lithification obviously proceeded without the assistance of wave activity in this extremely protected setting. The buildup of ammonium by-products resulting in the precipitation of

calcium carbonate here may have been due to the decay of significant amounts of fecal deposition in the cave related to the high concentrations of fish over the cave opening.

This then calls into question the actual role of wave activity in the lithification of reef substrate, especially since submarine lithification occurs by and large in shallow subsurface settings where skeletal debris is easily trapped pumped into the substrate (Ginsburg et al., 1971b; Macintyre and Glynn, 1976; Macintyre, 1977). Undoubtedly, organic debris would also be pumped by waves into the substrate, and this debris would slowly decay to yield ammonium carbonate and lead to the precipitation of the characteristic micritic crusts containing sediment grains (Macintyre and Marshall, 1988).

The decay of organic tissue has also been cited as a factor in the lithification of Red Sea reefs, along with the removal of carbon dioxide by the "photosynthesis and respiration of the biomass of the reef" (Friedman et al., 1974, p. 816). Some laboratory experiments support the idea that high pH levels can result from "photosynthetic activity in seawater trapped in corals and algal meadows" (Epstein and Friedman, 1982, p. 165).

Other possible entities contributing to the formation of carbonate cements are sulfate-reducing bacteria (Pigott and Land, 1986). However, their role is likely to be very limited because well-lithified reef deposits show little evidence of the iron monosulfides or pyrite expected from the release of hydrogen sulfide associated with such bacterial activity.

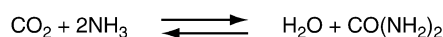
## Conclusions

Submarine lithification is a widespread phenomenon that binds the framework of coral reefs with cement produced in a marine setting. The resulting lithified structure consists mainly of micritic Mg-calcite in the form of crusts or heavily multibored and multicemented pavement limestones. Aragonite is a minor component of lithified structures in shallow waters but becomes more dominant in the deeper reef slopes. The mole percent  $\text{MgCO}_3$  of this Mg-calcite ranges from 14 to 19%, and the strontium content of the aragonite ranges from 6,900 to 10,500 ppm. The factors that induce submarine lithification are still not entirely clear. However, the decay of organic material does appear to play an important role in yielding an ammonium carbonate by-product that results in the precipitation of carbonate cements.

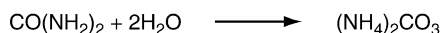
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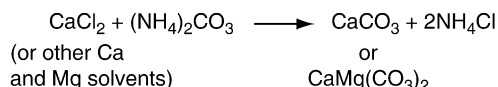
Urea is formed when carbon dioxide reacts with ammonia produced by organic decay



Some of this urea can react slowly with water to form ammonium carbonate



Ammonium carbonate then reacts with calcium chloride and other calcium or magnesium solvents to precipitate calcite or aragonite



**Submarine Lithification, Figure 4** Chemical reactions proposed by Towe and Malone (1970) for the precipitation of Mg-calcite and aragonite from seawater by ammonium by-products formed by organic decay (Macintyre and Marshall, 1988).

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## Cross-references

Aragonite  
 Bioerosion  
 Calcite  
 Diagenesis  
 Holocene Reefs: Thickness and Characteristics  
 Micrite  
 Platforms (Cemented)  
 Porosity Variability In Limestone Sequences  
 Reef Front Wave Energy

## SUBMERGED REEFS

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## Synonyms

Drowned reefs; Fossil reefs; Give up reefs; Relict reefs; Shelf edge reefs

## Definition

Submerged reefs are reefs formed during periods of lower sea level, which currently have little or no modern upward coral framework accretion. These reefs are found in water depths ranging from 25 to 2,000 m depending on their tectonic setting, but most commonly between 40 and 120 m on passive continental margins. They are thought to have drowned as a result of inimical environmental conditions associated with sea level rise during the last deglaciation.

## Introduction

Glacial and interglacial cycles have driven sea level oscillations over the last 500 ka, with extremes of at least –120 to +5 m relative to the present day sea level. Since the last glacial maximum of 19–20 ka, sea level has risen approximately 120 m (see Chapter *Postglacial Transgression*). Within this time period, episodes of dramatically faster sea level rise punctuated an otherwise fairly steady transgression (see Chapter *Meltwater Pulses*). The impacts of this extreme environmental change on reefs were varied and often detrimental to coral growth, including rapidly

increased depth and re-suspension of sediments during flooding of the shelves (see Chapter *Sea Level Change and Its Effect on Reef Growth*). These inimical conditions acted to slow the rate of reef accretion while sea level rise put them outside of the zone of optimal growth. Today, submerged reefs may have live coral cover in some cases, yet they are not believed to be making significant vertical progress towards the sea surface (e.g., Harris et al., 2004).

Submerged reefs have intrigued researchers since their earliest detection at the turn of the twentieth century (e.g., “submerged barrier reefs” of Barbados, Jukes-Browne and Harrison, 1891). Scientific interest accelerated in the late 1960s when these submerged reefs began to be readily interpreted as products of lower sea levels (e.g., Macintyre, 1967). It was not long before their worth as archives of past environments and climates was recognized, and with their associated corals, came to be firmly established as reliable records of palaeoenvironmental changes (e.g., Montaggioni and Macintyre, 1991) and rapid sea level fluctuations (Fairbanks, 1989). More recent studies are beginning to reveal the subtle complexities of climate and environmental change that have shaped the formation of each of these relict reefs (for a review, see Montaggioni, 2005).

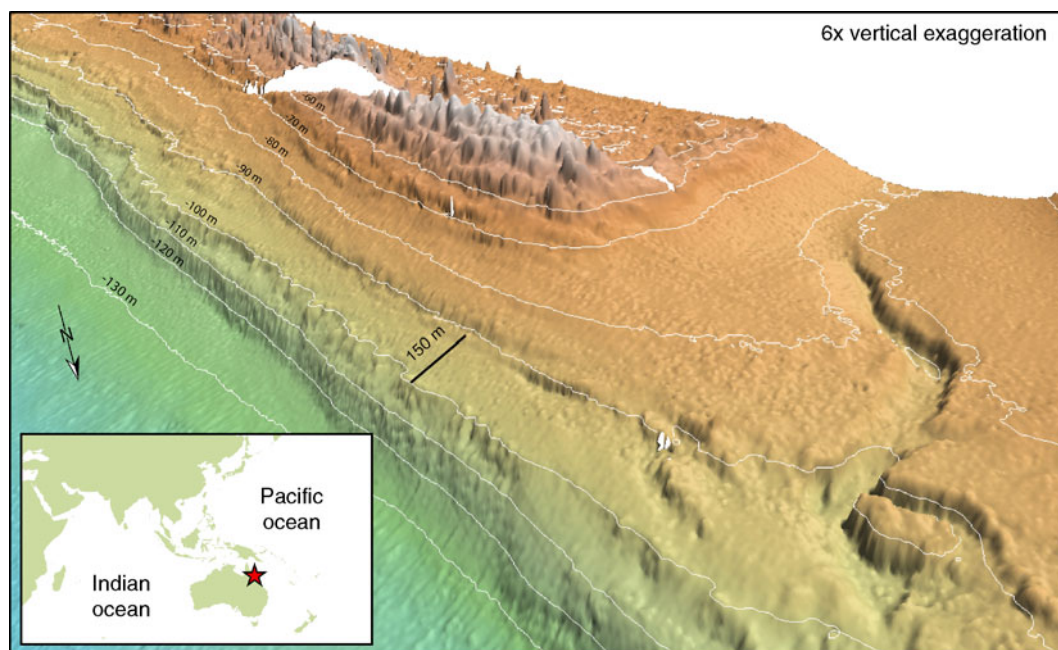
## Tectonic setting and geology

Submerged reefs can be divided as follows into three broad categories based on their geologic and tectonic setting: (1) reefs lying on stable continental margins, shelves, or platforms (e.g., The Seychelles, in the Indian Ocean, are composed of granitic continental crust and not the typical volcanic material of mid-plate oceanic islands, such as Hawaii or Tahiti.) with no significant vertical movement; (2) reefs lying on active tectonic margins with significant vertical movement, and (3) reefs surrounding subsiding oceanic islands.

Well-documented submerged reefs of passive continental margins include those of southern Florida, Australia's Great Barrier Reef, the Laccadive Islands, and other reefs off India's western margin. These submerged features display a wide range of morphologies, including terraces, barrier reefs, platforms and shoals, pinnacles and patch reefs, and reef-related features such as palaeo-lagoons (e.g., Figure 1). A commonality among many passive margin features is their great extent and continuity. India's continental margin contains 1,300 km of intermittent submerged reefs (Vora et al., 1996), and terraces on the outer shelf of the Great Barrier Reef have been observed to extend for hundreds of kilometers along the shelf edge (Hopley et al., 2007 pp. 285–296; Beaman et al., 2008). They generally range in depth from 25 to 120 m.

Submerged barrier reefs and terraces are also commonly found on slowly subsiding mid-plate oceanic islands, such as Tahiti, Hawaii, Marquesas, and Mayotte. As is the case on the islands of Hawaii, submerged reefs can be found at extreme depths as well, ranging from several hundred to nearly 1,500 m below sea level, depending on the rates of subsidence (Ludwig et al., 1991; Webster





**Submerged Reefs, Figure 1** Bathymetric map of the shelf edge near Noggin Pass, Great Barrier Reef, surveyed onboard the RV *Southern Surveyor* (SS07/2007). Area is gridded at 5 m<sup>2</sup> resolution and displayed using IVS3D Fledermaus. Images reveal extensive submerged terraces, pinnacles, and platform features along the shelf edge, as well as the existence of a possible palaeo channel. White represents no data. Note that scale varies with perspective view.

et al., 2004) (see Chapter *Hawaiian Emperor Volcanic Chain and Coral Reef History*). This is possible as much older Pleistocene reefs were never sub-aerially exposed during sea level regression of the last glacial period, and have been preserved in the rock record. As islands subsided and sea levels retreated at similar rates, reefs remained underwater and continued to grow. Subsequent island subsidence and sea level rise during the last deglaciation are responsible for the great depths at which these reefs are found today.

Zones of active tectonism are less commonly associated with submerged reefs, yet these relationships do occur. Barbados is one of the best known examples of slowly uplifted submerged reefs. The island is positioned on an accretionary prism with vertical movement of  $\sim 34 \text{ cm kyr}^{-1}$  (Fairbanks, 1989); however, the rate of deglacial sea level rise outpaced uplift and accretion, and these reefs were left submerged. With much time and continued uplift, they will theoretically break the sea surface and become sub-aerially exposed in the distant future (see Chapter *Emergent Reefs* and *Huon Peninsula, P.N.G.* as an example). An alternative scenario includes the rapidly subsiding reefs found in the Huon Gulf, Papua New Guinea. The combined effects of sea level rise and rapid subsidence have submerged these reefs to depths of  $\sim 2,000 \text{ m}$  (Webster et al., 2009).

### Submerged reef morphology

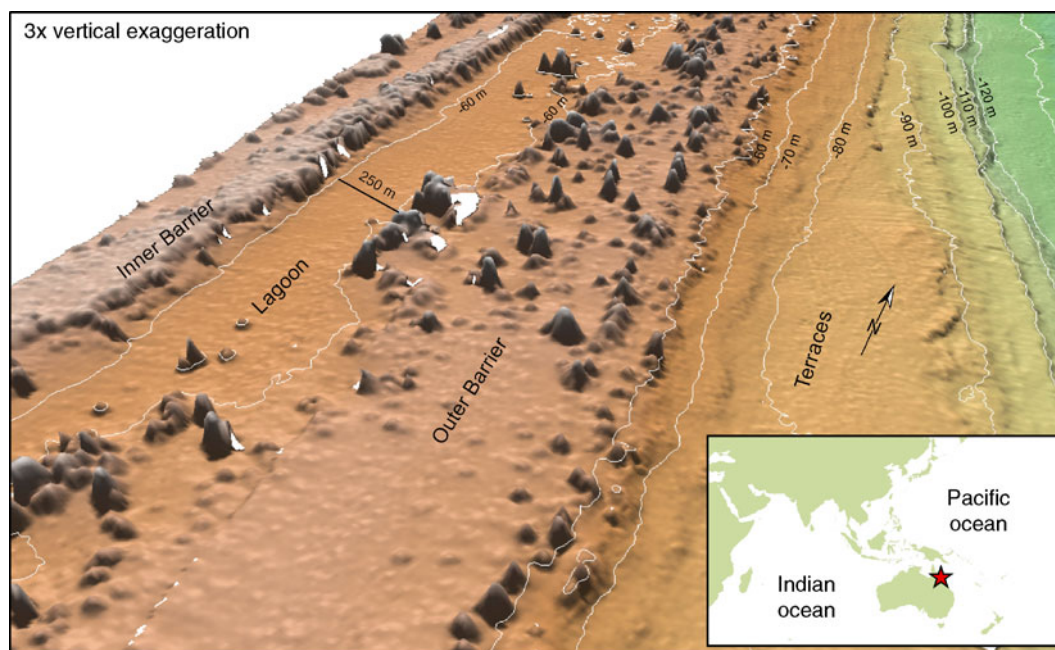
Morphological variations observed in submerged reefs are comparable to modern shallow reefs. High-resolution

bathymetry datasets, such as that seen in Figure 1, are the most accessible method of analyzing sea floor topography and any reef features. For instance, steep-sided pinnacle structures are thought to be submerged patch reefs (see Chapter *Patch Reefs: Lidar Morphometric Analysis*), and raised ridges or an extensive row of partially joined pinnacles are thought to be submerged barrier reefs (e.g., Figure 2) (see Chapter *Barrier Reef (Ribbon Reef)*). Recent work classifying reef features in a quantitative manner will make the task of standardizing terminology more attainable (Zieger et al., 2009).

Submerged reef morphology is thought to be influenced by palaeo-sea level variations (e.g., Brock et al., 2008) but also by the complex history of multiple phases of growth and erosion through many glacial and interglacial cycles (e.g., Beaman, Webster et al., 2008). The buried boundaries between depositional phases can be detected and mapped using seismic emissions which penetrate the substrate and show variations in reflectivity between lithologies (see Chapter *Seismic Reflection*). This type of information can provide insight into the morphology of the sea floor and basement prior to reef initiation and how its shape has influenced subsequent reef development.

### Geological significance

Submerged reefs carry great significance as recorders of past geological and environmental or climatic events. The unique physical properties of fossil corals and their ecological tolerances have made them useful to many



**Submerged Reefs, Figure 2** Submerged reef structures on the shelf edge near Noggin Pass, Great Barrier Reef. Identified features include parallel barrier reefs comprised of a raised ridge and pinnacles, a lagoon containing patch reefs, and seaward terraces. Gridding and display as per Figure 1, however, note 3× vertical exaggeration. Scale varies with perspective view.

studies, for example, as proxies for oceanic conditions (see Swart and Grottoli, 2002 for a review of recent work). After death, their hard skeletons, comprised of calcium carbonate ( $\text{CaCO}_3$ ), are readily preserved in situ, and environmentally driven isotopic fractionation and trace element ratios within their skeletons can be calculated (see Chapter *Palaeoclimate from Corals*).

Often, modern corals are used for recent climate reconstruction (see Grottoli and Eakin, 2007 for a discussion of  $\delta^{18}\text{O}$  and  $\Delta^{14}\text{C}$  records), but fossil reefs can extend the known record of climatic variations, and in particular submerged fossil reefs, as they tend to offer more pristine material than those subjected to the diagenetic effects of meteoric water and sub-aerial exposure. One very powerful property of corals is their capacity to be reliably dated using both radiocarbon and uranium series methods (see Chapter *Radiocarbon ( $^{14}\text{C}$ ): Dating and Corals* and *Uranium Series Dating*). When used in tandem with climate proxy records, much older high-resolution (on the order of seasonally or yearly) historical climate data can be obtained from these deeper submerged reefs. This method is particularly insightful when identifying oceanic conditions prior to reef death, as it may be compared to the prevailing conditions on today's modern reefs.

Reefs are also particularly useful for reconstructing past changes in relative sea levels. It is well understood that many corals (Done, 1982) and associated coralline algae (Adey, 1986) have narrow depth, energy, and water quality tolerances (see Chapter *Corals: Environmental*

*Controls on Growth and Fossil Coralline Algae*), making them excellent recorders of historical oceanographic conditions, sea level fluctuations, and tectonic movements. Scientific drilling has been the preferred method of investigation into submerged reefs for sea level reconstruction, as current technology makes it a relatively noninvasive endeavor in sensitive and protected ecosystems (see Chapter *Reef Drilling*). Drilling can often reveal the entire postglacial sequence of coral growth and subsequent death. Significant changes observed in these coral reef communities through time can be interpreted in the context of environmental and sea level fluctuations, in some cases revealing catastrophic events, such as the meltwater pulses (1A and 1B) seen in the Barbados reef record (Bard, 1990). However, local tectonics and isostatic response can produce conflicting sea level signatures across the globe. The Integrated Ocean Drilling Program (IODP) has recently completed large-scale drilling operations of submerged reefs on Tahiti (IODP Expedition 310 “Tahiti Sea-Level” in 2005, see Expedition 310 Scientists, 2007) and the Great Barrier Reef (IODP Expedition 325 “Great Barrier Reef Environmental Changes” in 2010, see Webster et al., 2009). As more reefs are investigated, further reconciliation of sea level curves across wide geographic areas can be achieved. For a comprehensive review of Indo-Pacific drilling and interpretation of reef facies, see Montaggioni (2005).

Large-scale morphological features detected with remote sensing technologies also provide geological and

sea level information. Parallel sequences of submerged terraces have been interpreted as reef backstepping due to sea level rise (see Chapter *Back-Stepping*). As the seas transgress inland, reefs re-establish themselves on newly submerged surfaces. Geophysics can also be used to detect large-scale features, such as the original surface upon which the reefs initiated. These surfaces are buried today, but subsurface seismic reflections can indicate their locations. By establishing the depth of the original substrate, reef thickness can be calculated, and with enough coverage, the general morphology of the older sea floor and basement substrate can be interpolated (see Chapter *Holocene Reefs – Thickness and Characteristics*).

However, caution must be taken when using corals to reconstruct global sea level fluctuations, as tectonic events can effectively raise or lower relative sea level. With this understanding and knowledge of global sea levels from more stable regions, submerged reefs can be useful for calculating the timing and amplitude of local subsidence or uplift. For example, the Hawaiian Islands' long history of tectono-volcanism can be observed in its coral reefs. Corals have been collected from great depths and dated to determine the rates of subsidence on the islands as well as to investigate the oceanographic properties of the larger Hawaiian-Emperor chain (see Grigg, 1997 for a review).

### Modern significance

The extreme depth of many submerged reefs has hindered modern ecological investigations because the costs and technology required to access such areas are often excessive. As a result, the understanding of mesophotic coral reefs (30 to 150 m water depth) has been slow to develop. While hermatypic corals generally thrive in shallow water environments (<20 m), light-dependent communities of corals, algae, and sponges have been documented at depths >100 m in the Caribbean, Hawaii, and Central Pacific (see Lesser et al., 2009 for a review on modern mesophotic reefs). Australia's living submerged reefs in the Gulf of Carpentaria (Harris et al., 2004) and the Great Barrier Reef (e.g., Webster et al., 2008) are presently the subjects of similar research. It is thought that these ecosystems may provide refuge habitats for reef biota during times of extreme environmental stress in the shallower regions (see Bongaerts et al., 2010 for a review). This retreat to deeper waters may have been a strategy corals have invoked during past sea-surface warming events. Shallow reefs may have been re-seeded by deeper refuge reefs post disturbance, staving off localized extinction events and adding a significant degree of resilience to these ecosystems. A lack of understanding and information about these deeper reef habitats has also precluded any significant organized management. These regions often lie outside restricted fishing and recreation areas, with governing bodies unaware of the existence of these habitats.

### Conclusions

The study of submerged reefs is invaluable to our knowledge of palaeoclimate, sea-level, and oceanographic processes. With an understanding of ancient reef response to climate disturbances, modern reefs subjected to today's stresses can be better managed. Rates of reef initiation and drowning can be calculated, and when coupled with palaeoclimate data, a more comprehensive understanding of controls on reef growth, development, death, and recovery can be attained (see Chapter *Historical Ecology of Coral Reefs*). Additionally, a number of these submerged reefs may provide modern reef habitats presently in need of management. The value of submerged and fossil reefs as proxies for modern reef response to global climate change is unparalleled, and as interest in historical reef records intensifies and technology improves, a more comprehensive understanding of submerged reefs will unfold.

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## Cross-references

Algae, Coralline  
 Back-Stepping  
 Barrier Reef (Ribbon Reef)  
 Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity  
 Corals: Environmental Controls on Growth  
 Carbonate Budgets and Reef Framework Accumulation  
 Earthquakes and Emergence or Submergence of Coral Reefs  
 Emerged Reefs  
 Fossil Coralline Algae  
 Hawaiian Emperor Volcanic Chain and Coral Reef History  
 Historical Ecology of Coral Reefs  
 Holocene Reefs: Thickness and Characteristics  
 Huon Peninsula, P.N.G.  
 Meltwater Pulses  
 Paleoclimate from Corals  
 Patch Reefs: Lidar Morphometric Analysis  
 Postglacial Transgression  
 Radiocarbon ( $^{14}\text{C}$ ): Dating and Corals  
 Reef Drilling  
 Sea Level Change and Its Effect on Reef Growth  
 Sea-level Indicators  
 Seismic Reflection  
 Swathe Mapping  
 Uranium Series Dating

## SUBSIDENCE HYPOTHESIS OF REEF DEVELOPMENT

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### Definition

The subsidence hypothesis of coral reef development was proposed by Charles Darwin and was formulated during his voyage on the *Beagle*. It envisaged that fringing reefs, barrier reefs, and atolls represent successive stages in an evolutionary sequence.

### Introduction

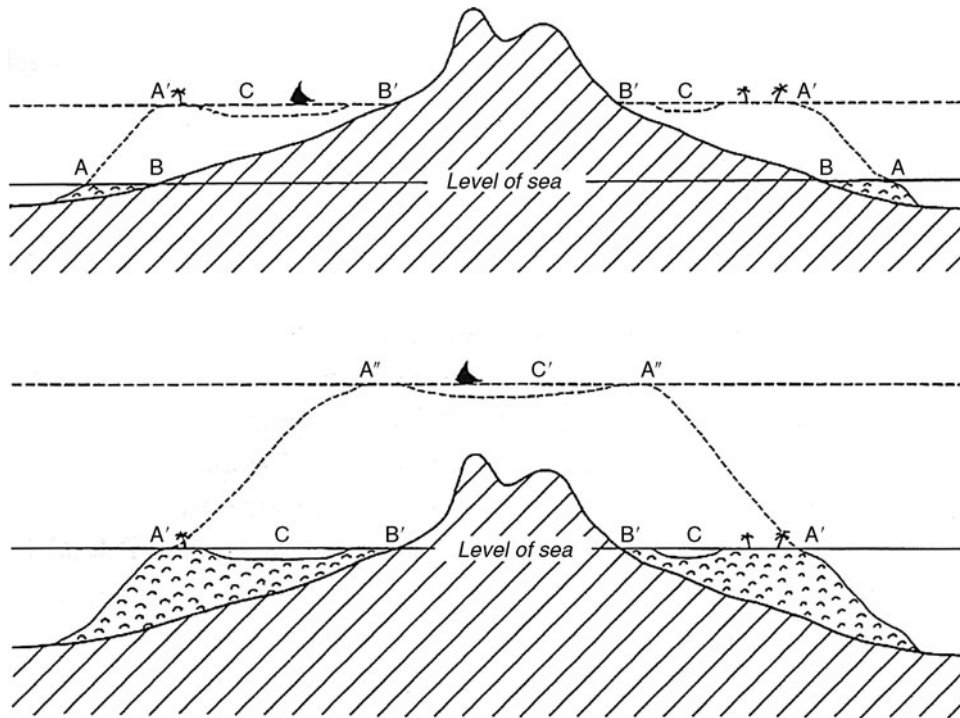
In a remarkable deduction, Charles Darwin proposed that different types of coral reef observed in mid ocean came about through the subsidence of underlying volcanic foundations. He envisaged that fringing reefs, barrier reefs, and atolls represented different stages as a result of vertical growth of reefs on subsiding basements. Subsequent drilling has provided support for this idea, which can be integrated into plate tectonic theory, and can also accommodate many factors associated with changes in sea level.

### Darwin's insight into atoll formation

At the time of Darwin's voyage on the *Beagle*, it was unclear how atolls had formed. A widely accepted view was that advanced by Charles Lyell who had proposed, in his *Principles of Geology*, which reached Darwin while on the voyage, that the annular rim of an atoll represented a coral veneer over the rim of a volcano (Lyell, 1832). Darwin formulated his "subsidence theory for reef development" shortly after leaving the coast of South America, where he saw evidence of marine deposits uplifted well above sea level and the aftermath of an earthquake, and before he encountered the numerous coral reefs of the Pacific.

Darwin proposed an alternative view: "namely the prolonged subsidence of the foundations on which the atolls were primarily based, together with the upward growth of the reef-constructing corals. On this view every difficulty vanishes: ...fringing reefs are thus converted into barrier-reefs; and barrier-reefs, when encircling islands are thus converted into atolls, the instant the last pinnacle of land sinks beneath the surface of the ocean" (Darwin, 1842, p. 109). As his sketch showed (Figure 1), these "three great classes" of reefs were stages in an evolutionary sequence, driven by gradual subsidence of the volcanic island around which the reef had initially formed.

Darwin had the opportunity to visit Tahiti in November 1835, from the slopes of which he looked over to the spectacular barrier reef surrounding neighboring Moorea. He refined his idea after leaving the Society Islands on his voyage to New Zealand (Stoddart, 1962). After the *Beagle* had visited Australia, it called at the Cocos (Keeling) Islands in April 1836. As this was the only coral atoll on which Darwin landed, he was keen to verify his hypotheses.



**Subsidence Hypothesis of Reef Development, Figure 1** Details of Darwin's original woodcut (1842) illustrating his subsidence hypothesis. In the upper diagram the original volcanic island is shown with a *fringing-reef* A-B. A section of reef and island after subsidence is given by *dotted lines*, which show an encircling *barrier-reef* with A' the outer edge of the reef, B' the shore of the encircled island, and C the lagoon channel between the reef and island's shore. In the lower diagram the newly formed barrier reef is represented by *unbroken lines*. As the island continues subsiding the coral reef will continue growing up on its own foundation, and after the sea covers the highest volcanic pinnacle a "perfect atoll" is formed with A'' representing the outer edge and C' the lagoon of the newly formed atoll (from McLean and Woodroffe, 1994, © Cambridge University Press, reproduced with permission).

His attention was drawn to erosion of the shoreline, and he regarded the undercutting of coconut trees "tolerably conclusive evidence" in support of his ideas.

On return to England, his geological observations on coral reefs were amongst the first of his results that he wrote up. He presented a paper to the Geological Society on May 31, 1837 (Darwin, 1838), and then produced a book on his observations on coral reefs, integrated with evidence extracted from charts of reefs he had not visited (Darwin, 1842). In this book, Darwin produced a map of the location of the reef types, atolls predominantly occurring in mid ocean, whereas fringing reefs were found around the margin of the Pacific in areas we now know to be plate-margin settings.

### Alternative theories

Darwin's subsidence hypothesis for reef development has played an important part in the historical development of reef formation ideas (Steers and Stoddart, 1977). A number of alternative hypotheses were proposed. For example, John Murray, influenced by his observations of deep-sea sediments during the *Challenger* expedition, believed that atoll lagoons formed through solution of carbonate, and that atoll reefs prograded around their margin

(Murray, 1880). Murray sponsored Guppy to visit the Cocos (Keeling) Islands, and in his detailed descriptions of the reef islands there, Guppy inferred evidence supporting progradation (Guppy, 1889).

Considerable support was expressed for Darwin's subsidence ideas, in particular, by Dana (1885), a member of the US Exploring Expedition to the Pacific Ocean, 1838–1842. He read about Darwin's ideas in a Sydney newspaper, and he became a fervent supporter of subsidence. Dana observed that shorelines of volcanic islands behind barrier reefs comprised a series of embayments implying that valleys had been submerged during subsidence. Later William Morris Davis, who had made such a major impact on geomorphology through his ideas of a geographical cycle, undertook an extensive review of the "coral reef problem," and possible explanations of how atolls had formed. Davis extended Dana's argument that embayments in volcanic shorelines represented drowned valleys and emphasized that there was insufficient detritus trapped in lagoons for erosion of the hillslopes to have occurred after the reefs formed. He expressed the view that Darwin's subsidence hypothesis was the most probable but that the only contender was that proposed by Daly (Davis, 1928).

Reginald Daly, who replaced Davis at Harvard, placed particular emphasis on changes in sea level that he realized had occurred during Quaternary ice ages. During glacial periods, when sea level was 100 m or more lower than present, Daly believed that atoll rims were entirely truncated, and modern rims had accreted vertically during the postglacial (Daly, 1915, 1925, 1934). A perceived regularity to the depths of lagoons was inferred to support this “glacial-control” view, which was strongly advocated by Wiens (1959, 1962). A glacially controlled subsidence hypothesis was advanced by Kuenen based on Indonesian reefs (Kuenen, 1933).

A number of studies came up with significantly different interpretations of reef formation. However, many of these were focused on reefs in tectonically uplifted areas, or continental margins, such as the Great Barrier Reef. Darwin’s subsidence hypothesis of reef development addresses oceanic reefs, and in particular, the formation of atolls, and the recognition that reefs from plate-margin settings deviate from this mode of evolution does not invalidate application of the subsidence model to oceanic reefs. Many of these anomalies were incorporated into subsequent editions of Darwin’s book “Coral Reefs”. Comprehensive reviews of these alternative ideas can be found in Cotton (1948), Hopley (1982), and Spencer et al. (2008).

One set of alternative hypotheses, that considered the form of modern reefs to be controlled by the older surfaces over which they had grown, deserves particular attention. Alexander Agassiz undertook a series of descriptive accounts of Pacific and Indian Ocean reefs (Agassiz, 1899, 1903). His observations were often superficial, interpreting reef blocks as outcrops of older underlying rocks, but he was convinced that modern reefs were a thin veneer over antecedent topography. Such ideas recur in the study of reefs; for example, Hoffmeister and Ladd (1944) proposed what they called the antecedent platform hypothesis. The significance of subaerial erosion and dissolution of emerged platforms exposed during glacial lowstands were emphasized by MacNeil (1954).

Shallow drilling of modern reef rims on atolls has frequently encountered an older reef limestone of Last Interglacial age, described below. Successive episodes of reef formation are separated with depth by a series of solutional unconformities. Exposure of these surfaces during glacial periods, when sea level was 100–120 m lower than present, and their karstification, form a major part of the antecedent karst hypothesis of Purdy (1974), which received much support from seismic profiling.

### Evidence from deep drilling

Darwin was aware that the strongest evidence to support his theory would come from drilling into the foundations of atolls, and he had written to Alexander Agassiz in 1881, “would that some doubly rich millionaire would take it into his head to have borings made in some of the Pacific and Indian atolls and bring back cores for slicing from 500–600 ft.” Such an attempt was made by the Royal

Society of London, together with Australian scientists on Funafuti (then part of the Ellice Islands, now Tuvalu). Between 1896 and 1898, expeditions to this atoll met with varying success. Under Sollas in the first year, coring reached 32 m, under Edgeworth David in the second year it reached 219 m, and under Finckh in the third year it finally reached 340 m (Spencer et al., 2008). At this depth, the substrate was dolomitic shallow-water carbonate; the underlying volcanic rock had not been encountered, but the recovery of shallow-water sediments at such a depth did provide some support for subsidence (McLean and Woodroffe, 1994).

However, it was postwar deep drilling on the Micronesian atolls of Bikini and Eniwetok, as part of atomic bomb testing, which encountered more than 1,000 m of limestones over a volcanic foundation that provided the strongest validation for the concept of gradual subsidence (Emery et al., 1954). Subsequent drilling on other atolls, such as Midway in the Hawaiian chain and Mururoa and Fangatafu in French Polynesia, provided further validation “with a certainty rarely obtained in geomorphology” (Guilcher, 1988, p. 70).

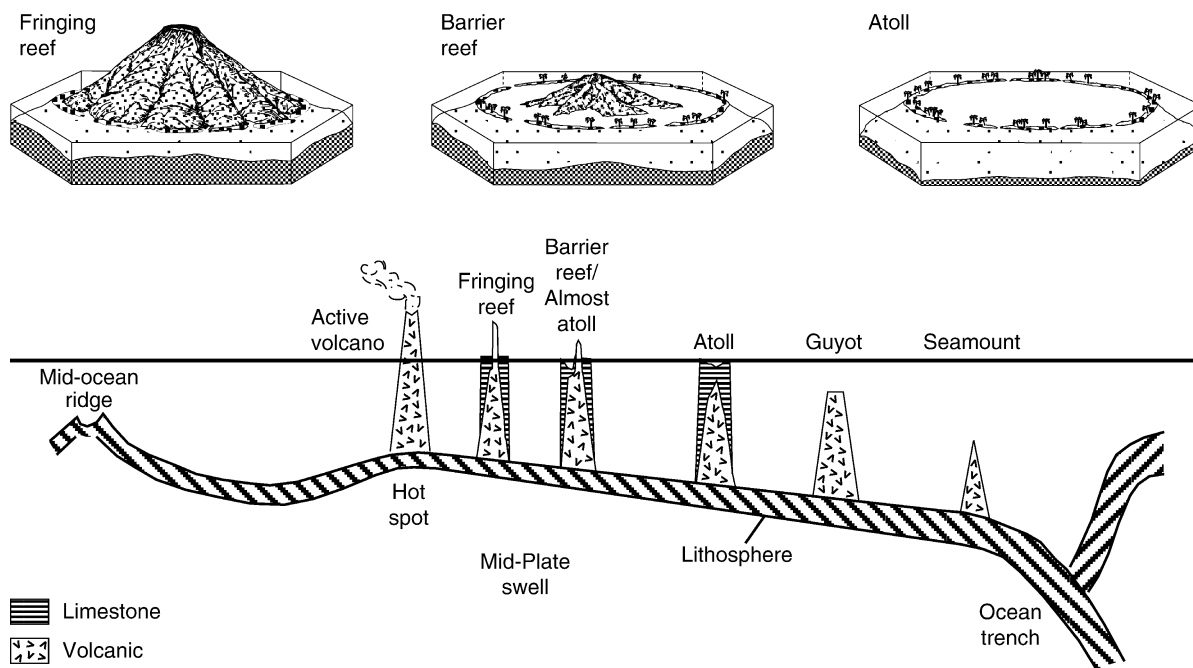
### Accommodating the subsidence hypothesis into plate tectonic theory

It has also been necessary to reconcile the idea of subsidence with the considerably enhanced understanding of the sea floor and plate tectonics. Atolls are frequently found in linear archipelagoes, and linear island chains are now understood to form as the ocean lithosphere moves over a “hot spot” (Scott and Rotondo, 1983). The Big Island of Hawaii is the best example of a young, volcanically active island. The successive high islands in the chain to the northwest of this island are progressively older. Subsidence can occur, both through isostatic adjustment of ocean crust to the mass of the volcanic island, the process that explains the rapid subsidence of the Big island, or through the gradual cooling and deepening of the plate as it migrates further from the mid-ocean spreading center (Figure 2). Thus, the islands in the Society Island chain, from Tahiti and Moorea to much smaller volcanic masses, such as Borobora and Huahine, represent this stage of barrier reef development. Atolls, such as those of the Tuamotu (though not in the same chain) are the ultimate stage, with the possibility that they may eventually become submerged as seamounts if the rate of vertical reef growth cannot keep pace with subsidence [as occurs beyond the latitudinal limit to reefs, a point called the Darwin Point (Grigg, 1982)].

### Sea-level fluctuations and the significance of karst erosion processes

Drilling through limestones that underlie atolls has revealed great thicknesses of shallow-water carbonates, confirming the continued, though interrupted, accumulation of limestone over the Cenozoic. However, during the Pleistocene, oscillations in sea level of 100 m or more





**Subsidence Hypothesis of Reef Development, Figure 2** Schematic examples of fringing reef, barrier reef, and atoll [based on the original sketches by Davis (1928)], and the relationship of such islands along a schematic linear island chain on the Pacific plate (after Scott and Rotondo, 1983). Linear island chains illustrate several of the stages; for example, the Big island of Hawaii represents an example of a volcanic island that is still active, and an incipient reef is forming on some shorelines. Oahu further along the chain has several former reef units, including elevated limestones of last interglacial age. A barrier reef is also represented by an almost atoll, where a volcanic island persists as a small outcrop of volcanic rock with a surrounding barrier reef, such as Aitutaki in the Cook Islands or Borabora in the Society Islands. There are numerous examples of atolls; some of the smaller islands in such archipelagos consist of a single island on a table reef. The lower diagram shows a schematic representation of how such islands might be distributed along an idealized chain, with plate motion from the spreading center (mid-ocean ridge) at the left, toward the ocean trench at the right.

have meant that there have been interruptions to the upward accretion of reef. It is necessary that there be accommodation space for sedimentation, and this is eliminated when the sea falls below the surface of the carbonate platform. Dating of sequences of the upper limestones has shown that these record successive highstands. The majority of reefs are underlain by a reef unit of Last Interglacial age (approximately 120,000 years BP, Thurber et al., 1965; Marshall and Jacobson, 1985; Woodroffe et al., 1991), which has been termed the Thurber discontinuity. This occurs at around 12 m below sea level on the Cocos (Keeling) Islands and around 15–20 m below sea level on many Pacific atolls. In several cases, this has been shown to be underlain by an older highstand (approximately 240,000 years BP, Szabo et al., 1985).

Exposure of the reef platform has meant an interruption in vertical accumulation of carbonate, but it is still the case that subsidence accounts for the larger thickness of limestones where there has been a greater rate of subsidence, and hence there has been a greater accommodation volume over time. However, it is less clear to what extent the platform has been denuded during these periods of exposure. The processes of karst erosion exert a major

control, and they act to lower the surface and have played a role in dissolution of atoll lagoons (Purdy and Winterer, 2001). Direct evidence in support of the transition from fringing reef to barrier reef and from barrier reef to atoll is also rare.

It is important to emphasize that the subsidence hypothesis is most appropriate for mid-ocean islands, whereas the largest barrier reefs such as the Great Barrier Reef and the Belize Barrier Reef are on continental shelves where Darwin's ideas are less likely to apply (Hopley, 1982). The role of dissolution of limestone on fringing reefs and barrier reefs is not adequately incorporated into the subsidence hypothesis (Purdy and Winterer, 2006). The significance of fluctuations in sea level was not realized when Darwin developed his ideas. It now seems clear that the transition from fringing reef to barrier reef is not as simple as portrayed in the schematic diagrams; indeed, there are many islands on which both fringing and barrier reefs occur around their margin. Furthermore, karst erosion processes have been extremely effective at producing barrier reef morphology, as on the makatea island, Mangaia in the Cook Islands, through solution of older reef units by percolation of rainwater across the underlying volcanic rock (Stoddart et al., 1985).

## Summary

Although the premise that uplift around the margin of an ocean might be balanced by subsidence beneath the ocean floor, which underpinned Darwin's hypothesis, is now seen to be simplistic and flawed, his remarkable deduction that such subsidence would give rise to three types of reefs, fringing reefs, barrier reefs, and atolls, has been broadly validated by stratigraphy and dating of cores through atolls. There are numerous exceptions to this sequence of development, particularly for those reefs on continental margins or that have experienced uplift. Nevertheless, gradual subsidence characterizes ocean lithosphere as it migrates from mid-ocean ridge (spreading center) to ocean trench. Although fluctuations in sea level have punctuated the development of atolls, with periodic exposure and karstification of the carbonate platform, gradual subsidence has persisted with successive veneers of reef limestone added during each highstand. There seems little doubt that this powerful hypothesis can be extended to explain the broad evolution of many mid-ocean atolls for which coring has not yet confirmed an underlying volcanic basement.

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[Accommodation Space](#)  
[Agassiz, Alexander \(1835–1910\)](#)  
[Antecedent Platforms](#)  
[Atolls](#)  
[Barrier Reef \(Ribbon Reef\)](#)  
[Bikini Atoll, Marshall Islands](#)  
[Cocos \(Keeling\) Islands](#)

[Darwin, Charles \(1809–1882\)](#)  
[Darwin Point](#)  
[David, Tannant Edgeworth \(1858–1934\)](#)  
[Davis, William Morris \(1850–1934\)](#)  
[Fringing Reefs](#)  
[Funafuti Atoll](#)  
[Lyell, Charles \(1797–1875\)](#)  
[MacNeil, F. Stearns \(1909–1983\)](#)  
[Midway Atoll \(Hawaiian Archipelago\)](#)  
[Mururoa Atoll](#)  
[Pacific Coral Reefs: An Introduction](#)  
[Plate Tectonics](#)  
[Reef Drilling](#)  
[Reef Structure](#)  
[Solution Unconformities](#)  
[Tahiti/Society Islands](#)  
[Volcanic Loading and Isostasy](#)

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## SWATHE MAPPING

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### Synonyms

Multibeam Mapping; Multibeam Sonar Mapping

### Definition

*Swathe mapping.* A technology used for the detailed 3D mapping of the seabed utilizing a vessel-mounted multibeam sonar that transmits a fan, or swathe, of acoustic energy across the ship track; then resolves multiple depth points across the swathe based upon the slant range and elevation angle of reflected echoes from the seafloor. Lidar is a similar technology to multibeam but using airborne laser bathymetry to swathe map shallow clear waters.

### Multibeam sonar

Singlebeam echo sounders have been applied routinely for many years to collect bathymetric or depth data from the world's oceans. This acoustic technique relies on a vessel-mounted transducer to generate a single acoustic pulse directed toward the seabed underneath the vessel. The echo sounder then calculates a depth measurement based on the travel time for the reflected seafloor echo to return to the receiver and speed of sound through water (Kunzig, 2000). During the 1970s, development began on multibeam sonar systems that use a multielement transducer array to transmit a fan, or swathe, of acoustic energy across the vessel's track. The swathe is narrow in the along-track direction, typically 1–2°, and wide in the across-track direction, generally 120° or more (Blacquire and van Woerde, 1998). The transmitted acoustic pulse frequency ranges from higher frequencies up to 450 kHz for mapping shallow coastal waters and the continental shelf, down to lower frequencies of 12 kHz for mapping the deep abyssal seafloor (Wille, 2005).

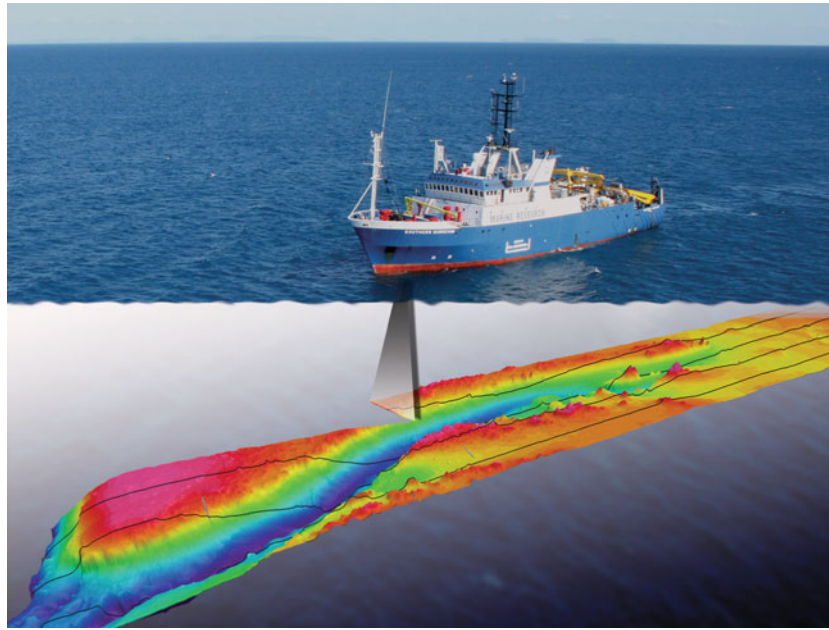
The multibeam receiver array measures the slant range and elevation angle of multiple seafloor echo returns across the swathe, and usually the echo strength of the returns which is called backscatter or amplitude. The multibeam sonar system also tracks the precise position of the vessel and motion data, such as gyro heading, heave, pitch, and roll, to calculate an accurate depth and position for the individual depth soundings. The number of depth measurements across the swathe varies between instruments but can be hundreds to thousands of soundings per second (Lekkerkerk, 2006). As long as the vessel is moving forward relative to the seabed, a multibeam swathe survey results in a dense “point cloud” of soundings that can be used to generate a 3D depth model, which accurately maps the underwater landscape (Figure 1). The resolution of seabed features that can be detected in such depth models can be sub-meter in size for shallow waters. However, in deeper waters, the resolution of observed features reduces to tens of meters due to the spreading properties of acoustic energy over longer distances and the lower frequencies used to ensonify the seafloor (Wille, 2005).

### Lidar

A similar seafloor mapping technique to multibeam sonar is the use of airborne laser bathymetry, or light detection and ranging (lidar), which use low-flying aircraft to scan pulsed laser beams across the seafloor and generate a swathe of depth soundings (Guenther, 2007). For example, the laser airborne depth sounder (LADS) uses a narrow infrared (1,064 nm) beam fired directly at the sea surface beneath the aircraft but does not penetrate the water, and thus reflects directly back to aircraft for calculating the aircraft's height above the water. A scanning mirror reflects a second green (532 nm) laser that tracks back and forth across the flight path in a grid pattern. The scanned green laser penetrates the water column to a limit of about 50–70 m (in clear water) that reflects off the seabed, if lying within this depth limit. The airborne receiver detects any reflected green laser signals and converts the returned signals into multiple depth points after subtracting the aircraft height value obtained from the infrared laser (Guenther, 2007).

Data density and acquisition rates vary between lidar instruments but typically collect about 1,000 depth soundings per second, with a swathe width of 200 m while flying at a height of about 500 m. At this height, the green laser beam footprint at the sea surface is about 2 m while the actual grid spacing can vary from 2 to 10 m apart. With aircraft speeds of about 150–175 km, lidar can deliver fast, high-resolution, shallow water surveying capabilities compared to vessel-mounted multibeam sonar systems (Guenther, 2007). The major disadvantage of lidar compared to multibeam is that laser signals are highly attenuated in turbid water and, therefore, lidar is ideally suited for surveying only in clear shallow waters. However, tropical coral reef areas provide additional navigational





**Swathe Mapping, Figure 1** Composite image showing the 3D effect of swathe mapping an ancient river channel incised into the Great Barrier Reef shelf, Australia, using a vessel-mounted multibeam sonar system. Grid pixel resolution is 5 m. Total grid distance is about 8 km.

dangers to vessels conducting multibeam surveys, and so lidar has been used to successfully map large areas of continental shelf where vessel surveys would be impracticable (Figure 2).

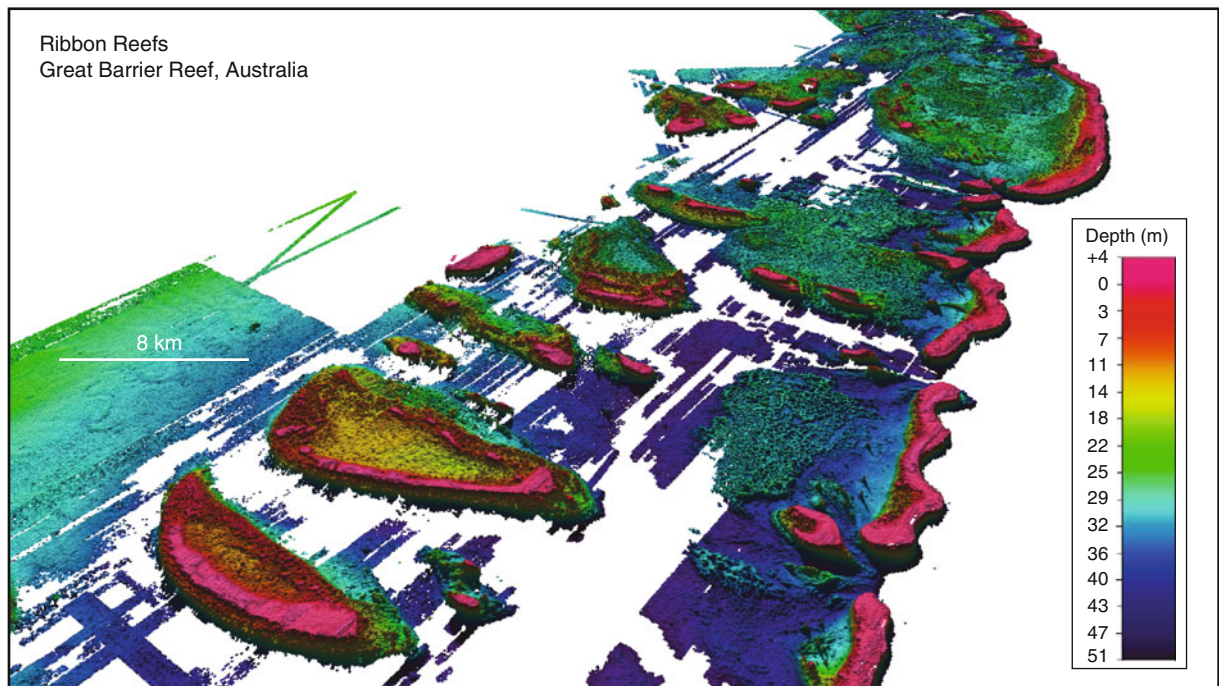
### Examples

The development of the various swathe mapping technologies represents an evolution in the ability to image large areas of the seafloor in nearly as high a detail as found in aerial photographs of land (Wille, 2005). For state mapping agencies, these advanced technology mapping tools provide the density of soundings to detect fine-scale shoal features that pose risks to maritime navigational safety (see Australian Hydrographic Service; <http://www.hydro.gov.au/aboutus/what.htm>). For industrial and scientific purposes, this evolution in ocean mapping technology reveals the true shape and geological nature of the seafloor (Figure 3). For coral reef environments, swathe mapping has provided new insights about the geomorphology of coral reefs and the inter-reefal seafloor beyond the limits of scuba diving (e.g., Grigg et al., 2002; Finkl et al., 2005; Beaman et al., 2008; Brock et al., 2008; Webster et al., 2008). Combined with other remote sensing techniques, such as sub-bottom profilers and towed sidescan sonar, and optical and sediment ground-truth methods, the detailed seabed habitat maps are a fundamental first step on which to base management decisions about coral reef ecosystems (see Pacific Islands Benthic Habitat Mapping Center; <http://www.soest.hawaii.edu/pibhmc/>).

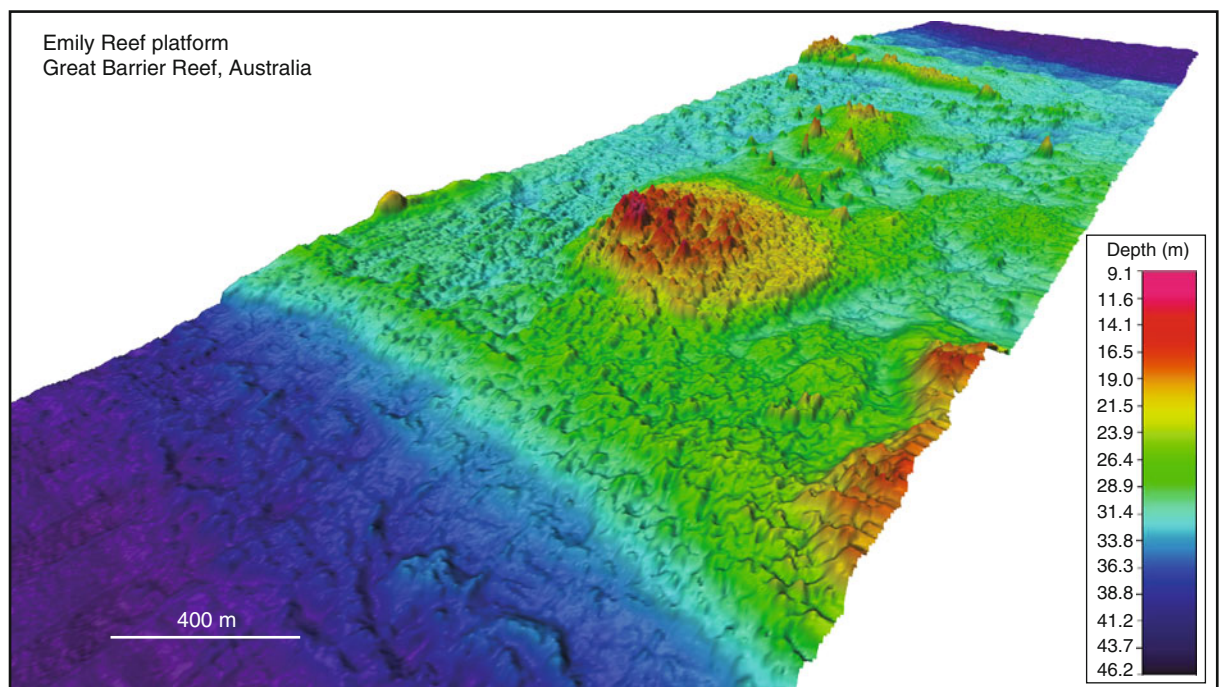
### The future

Future improvements in swathe mapping technology will increasingly see multibeam sonar systems mounted on underwater vessels, such as remote operated vehicles (ROVs) and untethered autonomous underwater vehicles (AUVs; Mayer, 2006). The advantage of taking a multibeam system closer to the seafloor are improvements in the quality of acoustic returns, but these methods also provide engineering challenges for the accurate positioning and orientation of the vessel within the water column. Other mapping advances will see greater use of multifrequency (hyperspectral) acoustic and laser transmissions which allow improved generation of co-registered seafloor reflectance (substrate) imagery, as well as mid-water feature detection, such as schools of fish and gas seeps. Advances in the development of interactive 3D visualization software will also be seen in order to facilitate the interpretation and analysis of these large, complex, multicomponent spatial datasets (Mayer, 2006).

Additional future challenges are more political in nature. Developed nations with access to these tools will need to provide greater assistance to developing coastal nations, many of which have jurisdiction over vast ocean areas with sensitive coral reef environments. These developing nations often lack the human resources, mapping skills, and equipment to help solve their own environmental problems, and therefore developed nations must assist in the technology transfer to generate the spatial datasets necessary for informed coral reef management decisions (see Pacific Islands Applied Geoscience Commission; <http://www.sopac.org/homepage>).



**Swathe Mapping, Figure 2** Lidar mapped Ribbon Reefs in the northern Great Barrier Reef, Australia. The gaps in data coverage are inter-reefal areas where seabed depths lie greater than about 50 m, the limits of laser penetration into the water column. Grid pixel resolution is 25 m. Total grid distance is about 110 km.



**Swathe Mapping, Figure 3** An example of a multibeam swathe mapping survey over Emily Reef, a broad coral reef platform on the northern Great Barrier Reef, Australia. Grid pixel resolution is 5 m. Total grid distance is about 8 km.



## Conclusion

Swathe mapping techniques, such as multibeam and lidar, have provided an evolution in mapping of the world's oceans over the past few decades. For tropical coral reefs, swathe mapping provides greater understanding about the true nature of the deeper seabed and inter-reefal habitats. These new discoveries are guiding major advances in energy extraction, fisheries resource management, and environmental protection of the sea. Developed nations with access to these tools must provide technology transfer to the developing coastal nations that have jurisdiction over sensitive coral reef environments, but still lack the human resources, mapping skills and equipment to help solve their own environmental issues.

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## Cross-references

AUVs (ROVs)  
 Remote Sensing  
 Seismic Refraction  
 Submerged Reefs

## SYMBIOSIS

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## Synonyms

Mutualism

## Definition

The close and usually long-term interaction between members of different biological species. From the greek words *syn* (together) and *biosis* (living): “living together.”

Originally introduced by Anton de Bary in 1879 to refer to “the living together of differently named organisms,” symbiotic relationships include mutualisms (in which both partners mutually benefit from the interaction), parasitisms (in which one partner benefits at the expense of the other), and commensalisms (in which one partner benefits and the other partner is unaffected). However, in both scientific literature and the vernacular, “symbiosis” is often used to refer strictly to mutualistic interactions (Wilkinson, 2001).

Symbioses (including mutualisms, parasitisms, and commensalisms) are particularly common on modern coral reefs, where species densities and the incidence of coevolved relationships are extraordinarily high. Perhaps the most critical mutualistic symbiosis on modern coral reefs is that between scleractinian reef corals and dinoflagellates in the genus *Symbiodinium*, commonly referred to as “zooxanthellae.” These algal symbionts live in the gastrodermis of the coral (hence are “endosymbionts”) at densities that typically reach 1–2 million per square centimeter of coral tissue, and pass >90% of the energy-rich products of their photosynthesis (photosynthate) to their host (see Chapter *Zooxanthellae*). This mutually beneficial arrangement drives the high productivity found on coral reefs and sustains the rapid calcification and growth of corals that in turn build the reef and create the habitat which supports the high biodiversity characteristic of these ecosystems (Muscatine and Porter, 1977). Mutualisms involving reef corals and Bacteria are also a growing area of symbiosis research, with some Bacteria hypothesized to benefit coral hosts by, for example, producing antibiotics (Reshef et al., 2006).

Another example of a common mutualistic symbiosis on reefs is that of “cleaning stations”, where small fish (*Labroides* spp.) and shrimp remove parasites from the body, mouth, and gills of larger fish. Cleaners are recognized by their bright coloration patterns and behaviors, and large fish congregate at cleaning stations – usually coral outcrops or other prominent reef features – to benefit from these services (Grutter, 1999). Other well-studied examples of coral reef mutualisms include the association between clown fish (*Amphiprion* spp.) and large sea anemones. The clown fish (and some other related species in the genera *Premnas* and *Dascyllus*) do not trigger the anemone's stinging response, and receive protection from



predators by using the anemone as a home base. In return, the bright colors and aggressive behavior of the fish attract other fish, which then become potential prey for the anemone.

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Wilkinson, D. M., 2001. At cross purposes. *Nature*, **412**, 485.

### Cross-references

[Microbes](#)  
[Temperature Change: Bleaching](#)  
[Zooxanthellae](#)

# T

## TAHITI/SOCIETY ISLANDS

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### Definition

The Society Islands are a group of aligned volcanic islands in the south Pacific, with Tahiti as the main island. Their name is usually thought to have been attributed by Captain James Cook in honor of the Royal Society of London. Politically speaking, these islands are part of the French Polynesia.

### Environmental setting

Located in the southern Pacific Ocean between 17°52'S–148°4'W and 15°48'S–154°32'W, the Society Islands are subdivided from southeast to northwest into the Windward Island Group (Mehetia, Tahiti, Moorea, Maiao, Tetiaroa) and the Leeward Island Group (Huahine, Bora-Bora, Raiatea, Tahaa, Maupiti, Tupai, Mopelia, Scilly, Bellinghausen). They result from the activity of a volcanic hot spot at present located close to Mehetia at the southeastern end of the island chain. The high volcanic islands increase in age from less than 0.3 to about 5 million years along a southeast–northwest axis (Guillou et al., 2005). Except for Mehetia, all these islands are surrounded by fringing and/or barrier reefs. The low-lying coral islands (atolls) include Tetiaroa, Tupai, Mopelia, Scilly, and Bellinghausen.

### Coral diversity and distribution

Compared to the world's richest Indonesian center, the scleractinian coral fauna at Tahiti and in the nearby islands appears substantially depauperate. The number of reef-building coral genera in the region does not exceed 35. Additionally, species richness varies substantially from

zone to zone. Species richness and coral cover rate decline from the open sea shorewards. Along fore-reef slopes, the coral pool contains up to 25 species. By contrast, in reef-crest and reef-flat zones, the number of species is less than 20 (Karlson et al., 2004).

The composition of the reef coral communities has been quantitatively analyzed in Moorea and regarded as exemplifying that of the Society high volcanic islands (Bouchon, 1985). Fringing reef flats are typified by paucispecific assemblages with massive, branching, and foliaceous forms (*Porites lutea*, *P. (Synarea) rus*, *Montipora circumvallata*, *Pavona cactus*). Barrier reefs exhibit higher diversity communities. The barrier reef flats are dominantly composed of robust branching, arborescent, and laminar acroporids (*Acropora abrotanoides*, *A. robusta*, *A. nobilis*, *Montipora erythraea*, *M. verrucosa*), pocilloporids (*Pocillopora verrucosa*, *P. damicornis*), and massive poritids (*Porites lobata*, *P. lutea*). The backreef zones are colonized preferentially by tabulate and laminar acroporids (*Acropora cytherea*, *Montipora erythraea*) and massive poritids. Along the fore-reef slopes, three distinct assemblages can be identified. The deeper fore-reef assemblage (>30 m) consists mainly of poritids (*Porites*, *Synarea*), faviids (*Leptastrea purpurea*, *Favia stelligera*), and agariciids (*Pachyseris speciosa*). The intermediate assemblage (15 to >20 m) is typified by poritids (*Napopora irregularis*) and faviids (*Montastrea curta*, *Leptastrea transversa*) together with agariciids (*Gardineroseris planulata*). The upper fore-reef community (<10 m) prominently contains acroporids (*A. humilis*, *A. intermedia*, *A. variabilis*, *Montipora erythraea*) and pocilloporids (*Pocillopora eydouxi*, *P. verrucosa*).

The coral distribution on the Society atolls is very close to that described from the high islands. Some differences are observed only in the composition of lagoonal patches. These are made up of *Pseudocolumastrea*, *Pavona*, *Stylophora*, *Stylocoeniella*, *Acanthastrea*, *Platygyra*, *Astreopora*, *Cyphastrea*, and *Psammocora*, associated with ubiquitous

forms (*Porites lobata*, *Leptastrea*, *Acropora* spp., *Pocillopora*). The reef-crest settings usually show a typical algal ridge about 0.5–1 m in elevation and dominantly composed of coralline algae (*Hydrolithon onkodes*, *Porolithon craspedium*). The coral coverage ranges from 2% to less than 10% of the substrate area. Corals include pocilloporids and robust acroporids.

### Stratigraphy, lithology, and growth history of late Pleistocene to Holocene reefs

The studies devoted to the internal structure and growth history of the Society Island reefs began with the use of subsurface drilling in the 1970s. Most of the drilling investigations have been conducted on Tahiti Island both through modern barrier reefs at sea level (Montaggioni, 1988; Cabioch et al., 1999) and submerged buildups at present located at 42–118 m water depth (Camoin et al., 2007). Uranium series dating of corals indicate that both coral reef systems consist of two distinct lithological sequences: a last deglacial sequence (Bard et al., 1996; Camoin et al., 2007) and an older Pleistocene sequence (Thomas et al., 2009).

#### The last deglacial sequence

This sequence started to deposit at about 16,000 calendar years BP and is 85–93 m in maximum thickness. The reef piles beneath the modern outer barrier reef flat are dominantly composed of rigid coralline frameworks thickly encrusted with microbialites, locally associated with vermetids and encrusting foraminifera or interbedded with detrital material (*Halimeda* plates mainly). Four main coralline assemblages have been delineated from base upwards: a branching/encrusting *Porites* (*P. nigrescens*, *P. lichen*) assemblage mainly encrusted with branching coralline *Lithophyllum* and *Mesophyllum*; a massive *Porites* (*P. lobata*, *P. lutea*) assemblage usually associated with branching *Lithophyllum* and *Dermatolothon*; a tabular branching *Acropora* (*A. hyacinthus* group, *A. clathrata*) assemblage with massive *Montastrea annuligera*, encrusted with millimeter-thick crusts of *Neogoniolithon* cf. *absimile*, *N.* cf. *propinquum*, *Dermatolothon* cf. *tesselatum*, and *Mesophyllum prolifer*; and a robust branching *Acropora* (*A. robusta* group, *A. humilis*) and *Pocillopora* (*P. verrucosa*) assemblage coated with 2–5-cm-thick veneers of *Hydrolithon onkodes* and *Neogoniolithon fosliei*. By analogy with the habitat depth range of their modern counterparts, these coralline communities are assumed to form a succession that reflects an upward-shallowing sequence. Furthermore, given that the robust branching *Acropora*–*Hydrolithon onkodes* assemblage usually occupy 50–85% of the total core length, the barrier reef top is thought to have maintained pace with the rising sea level during the main phases of reef accretion (keep-up growth mode).

The reef piles beneath the submerged buildups present strong similarities in composition to those described from the barrier reef. In addition to the four coralline communities delineated above, there have been found foliaceous

and laminar coral assemblages mainly composed of deep-water forms (*Montipora*, *Pachyseris*, *Echinophyllia*, *Leptoseris*) locally associated with a variety of ubiquitous genera (*Porites*, *Leptastrea*, *Astreopora*, *Psammocora*). These colonies are coated with millimeter-thick coralline algal crusts (mostly *Dermatolothon*, *Mesophyllum*, and *Lithophyllum*) in association with microbialites to form loose frameworks. This deep-forereef assemblage usually occur at the uppermost part of the core sections. Thus the coralline succession appears to be reversed compared to that of the barrier reef. This expresses upward-deepening conditions (give-up growth mode) in relation to a reef drowning event.

Microbialites are one of the major components of the deglacial reef sections, locally representing up to 80% of the reef rock (Montaggioni and Camoin, 1993; Camoin et al., 1999; Camoin et al., 2007). They have been encountered at all depths in the test areas and range in age from about 16,000 to 4,500 calendar years BP. Microbialites occupy the primary cavities within the reef rock and usually form a late stage of encrustation over coralline frameworks. They exhibit a suite of typical growth forms ranging from irregular domes and bulbs to columns. Their internal fabrics range from structureless dense micrite to clotted aggregates, resulting in two end-members represented by microbial laminae and thrombotic to dendritic structures. Composed of high-magnesian calcite with 7–16 mole%  $MgCO_3$ , they have developed principally through the activity of heterotrophic bacteria.

The coralline assemblages recognized in the Tahiti cores have been used as reliable paleodepth indicators. A coral-based sea-level curve has been reconstructed for the past 16,000 years (Bard et al., 1996; Camoin et al., 2007). Analysis of the curve indicates the presence of hiatuses in reef growth at around 14,000 calendar years BP. This provides strong support for a rapid sea-level jump interpreted as triggered by an important meltwater pulse (MWP-1A). By contrast, no detectable meltwater surge has been recorded in the reef cores at around 11,500 (MWP-1B) and 8,200–7,600 (8.2 ka event) calendar years. Sea level appears to have approximated its present position at around 6,500 calendar years.

#### The older Pleistocene sequence

The unconformity between the last deglacial and older Pleistocene sequences ranges in depth between 87 and 122 m below present sea level. Several successive unconformities are identified in the upper sections of the older Pleistocene sequence, indicating the superimposition of successive reef bodies. This is confirmed by chronostratigraphy. Uranium–thorium dating of pristine coral samples (Thomas et al., 2009) reveal active reef growth respectively between 153,400–152,700 years BP (Marine Isotope Stage (MIS) 6), 137,800–136,900 years BP (transition MIS 6–5), and 33,000–29,600 years BP (MIS 3). The older Pleistocene sequence is similar in composition to that of the last deglaciation. It is made up of several depth-related coralline



assemblages respectively dominated by tabular *Acropora*, massive *Porites*, encrusting *Montipora* and *Pachyseris*, and coated with thick microbialite crusts.

### Emerged reefs and related features

The Society Islands exhibit high sea-stand indicators including in situ emerged microatolls, abandoned algal ridges, and conglomerates. These give evidence of a mean sea-level standstill at a maximum elevation of +1.0 m between 5,000 and 1,200 years BP as a result of the postglacial hydro-isostatic adjustment. However, there are significant differences in the present elevation of the mid-Holocene shorelines between the Leeward and Windward Islands. The elevation ranges from about +1.0/+0.8 m from Scilly to Huahine to +0.5/+0.3 m in Tahiti and Moorea. This strongly suggests that since 3,000 years BP, Tahiti and Moorea have undergone a gradual subsidence at a rate of about 0.15 mm yr<sup>-1</sup>, which is interpreted as caused by a differing lithospheric flexuring along the island chain (Pirazzoli and Montaggioni, 1988).

There is no evidence of Pleistocene high sea stands regionally.

### Coral paleoclimatology

The measurement of growth characteristics over the last two centuries on *Porites* colonies collected from Moorea Island indicates that the average linear extension and calcification rate have increased significantly in response to increasing sea-surface temperature. The growth records show oscillatory modes at periods of about 21.9 and 4.5–6.6 years, respectively, attributed to changes in El Niño-Southern Oscillation and solar radiation (Bessat and Buigues, 2001). The regional record of a recent increase in sea-surface temperature is consistent with coral oxygen isotope data (Boiseau et al., 1998).

### Summary

The Society Islands, including Tahiti, form a linear chain of volcanic islands rimmed by fringing to barrier reefs and locally forming atolls. The coral diversity does not exceed 35 genera. Acroporids, pocilloporids, and poritids are the most common reef builders irrespective of island. Algal ridges are usual reef-crest features. The world's thickest continuous reef sequence encompassing the last deglacial times has been extracted from the Tahitian barrier reef. Late Pleistocene to Holocene reef frameworks are typified by the general occurrence of thick microbialite crusts. There are exposures of mid- to late Holocene reef-related deposits in most of the islands, providing evidence of a high sea stand at a maximum elevation of +1 m.

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### Cross-references

Conglomerates  
 Emerged Reefs  
 Holocene Reefs: Thickness and Characteristics  
 Microatoll  
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 Uranium Series Dating  
 Volcanic Loading and Isostasy

## TAPHONOMY

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### Definition

Taphonomy is the systematic study of the processes that affect organic material, including skeletons, postmortem.

### Introduction

The geologic subdiscipline of Taphonomy was introduced originally by Efremov (1940) to include the study of the processes involved in the transition of organic remains from the biosphere to the lithosphere. Over a five-decade interval (~1920–1970), numerous German researchers at the Senckenberg Research Institute of Marine Biology and Marine Geology on the North Sea carried out classic investigations of processes of decay, disarticulation, and burial affecting organisms in shallow marine environments. The results of those studies (Aktuo-paläontologie or “Paleontology of the Recent”) were compiled by Schäfer (1972) into a landmark volume. A generation of paleontologists in North America and the former Soviet Union subsequently began to elucidate and quantify the ecological information lost as organisms were subjected to a variety of physical, biological, and chemical processes prior to their final entombment within the sediment and subsequent discovery as fossils (e.g., Lawrence, 1968; Schopf, 1978). The results of such studies typically were issued in the form of a caveat to any researcher seeking to reconstruct communities based on the fossil record. This body of research is generally referred to as the “information loss” approach to taphonomic studies.

Research reports published in a taphonomy theme issue of the *Journal Palaios* (1986) demonstrated clearly that taphonomic processes that remove ecological information from the fossil record themselves yield preservable signatures characteristic of specific sedimentary environments and processes of deposition (e.g., Brett and Baird, 1986). This “information gain” approach to Taphonomy catalyzed another generation of paleontologic research that applied modes of preservation to paleoenvironmental reconstruction and temporal resolution of fossil assemblages and has dominated the literature over the last quarter century (extensive reviews are given in Allison and Briggs, 1991; Donovan, 1991; Martin, 1999, and Behrensmeyer et al., 2000).

### Reef coral taphonomy

Relative to other marine invertebrates that possess potentially preservable hard parts, coral preservation has received attention from paleontologists relatively late in the history of the subdiscipline. Although Martindale (1984) and Scoffin (1992) reviewed the salient taphonomic processes operating in coral reef environments, taphonomic research on the most important component of reef structures, the corals themselves, was largely lacking until the mid-1990s. Despite its relatively late appearance,

taphonomic research on coral reefs (for reviews see Greenstein, 2007; Perry and Hepburn, 2008) expanded rapidly in parallel with (and, in part, to justify) the increasing use of the Quaternary fossil record of coral reefs to better understand the various disturbances currently affecting modern reefs. The burgeoning reef taphonomic literature has documented a variety of important results which fall into five general categories: (a) sources of taphonomic bias affecting corals, (b) fidelity of coral death assemblages to life assemblages, (c) comparisons of the taxonomic composition of coral life, death and fossil assemblages, (d) using taphonomically important organisms and/or processes to determine depositional environments and history of reef framework accumulation, and (e) application of taphonomic and paleoecological data to provide a geological context for the current reef crisis (Table 1).

### Taphonomic bias

Studies of taphonomic bias affecting corals involve systematic quantification of a variety of features produced while dead colony skeletons reside on the sea floor. Although many of these features may either add carbonate material (e.g., encrusting skeletons of epibiont organisms) or remove it (e.g., borings made by a variety of endobiont organisms) all have the effect of inhibiting the potential for identification of a coral taxon. Several studies have investigated the roles that coral colony growth form and reef environment play in determining preservation potential of corals present in death assemblages of the Great Barrier Reef (Pandolfi and Greenstein, 1997a) and the tropical Western Atlantic (Greenstein and Pandolfi, 2003; Gardiner et al., 2005) regions. Perry (1998) elucidated the environmental distribution of macro-boring organisms (and hence, preservation potential of the affected coral skeletons) in adjacent reef environments across a barrier reef system in Jamaica. Results of these studies indicate that preservation potential is highly variable between reef environments and also that higher diversity coral assemblages (particularly acroporid corals with branching colony growth forms) in the Indo-Pacific region may suffer particularly from taphonomic bias.

### Fidelity

Fidelity refers to the degree to which any fossil assemblage reflects the taxonomic composition of a once-living assemblage (see Kidwell and Bosence, 1991). In marine environments, fidelity studies, typically, are conducted by systematically sampling and identifying live and dead organisms occurring in and on the substrate. An implicit assumption of these types of studies is that the death assemblage represents the “first step” in the transition of a living assemblage of organisms into the fossil record (Greenstein, 2007), although for corals, this may not be the case (Edinger et al., 2001).

Fidelity studies of coral assemblages began with comparisons of live and dead reef coral assemblages by Pandolfi and Minchin (1995) on fringing reefs in Madang Lagoon, Papua New Guinea. Live–dead comparisons of

**Taphonomy, Table 1** Summary of representative literature on coral reef taphonomy

| Type of study                                                     | Location                              | Reference                                      |
|-------------------------------------------------------------------|---------------------------------------|------------------------------------------------|
| Taphonomic biasing of reef corals                                 | Florida Keys                          | Gardiner et al., 1995                          |
|                                                                   | Bahamas                               | Greenstein and Pandolfi, 2003                  |
|                                                                   | Great Barrier Reef                    | Greenstein and Moffat, 1996                    |
|                                                                   | Jamaica                               | Pandolfi and Greenstein, 1997a                 |
|                                                                   | Indo-Pacific                          | Perry, 1998                                    |
| Fidelity of coral life assemblages to death assemblages           |                                       | Pandolfi and Minchin, 1995                     |
|                                                                   | Florida Keys, shallow reefs           | Greenstein and Pandolfi, 1997                  |
|                                                                   | Florida Keys, deep reefs              | Pandolfi and Greenstein, 1997b                 |
| Comparison of reef coral life, death, and fossil assemblages      | Bahamas, Florida Keys                 | Greenstein et al., 1998a, b                    |
| Paleoenvironmental reconstruction/history of framework deposition | Papua New Guinea                      | Edinger et al., 2001                           |
|                                                                   | Barbados                              | Martindale, 1992; Perry, 2001                  |
|                                                                   | Jamaica                               | Scoffin and Hendry, 1984; Perry, 1999, 2000    |
|                                                                   | Western Australia                     | Andresen and Greenstein, 2006                  |
|                                                                   |                                       | Clayton and Greenstein, 2005                   |
|                                                                   | Netherlands Antilles                  | Meyer et al., 2003                             |
|                                                                   | Great Barrier Reef                    | Perry and Smithers, 2006                       |
|                                                                   | Phuket, Thailand/Male Atoll, Maldives | Scoffin, 2000                                  |
|                                                                   | Gulf of Mexico                        | Blanchon and Perry, 2004                       |
|                                                                   | US Virgin Islands                     | Hubbard et al., 2005                           |
| Application to modern reef ecology                                | Belize                                | Aronson and Precht, 1997, 2001                 |
|                                                                   |                                       | Aronson et al., 2005                           |
|                                                                   | Jamaica                               | Precht and Aronson, 1997; Wapnick et al., 2004 |
|                                                                   | Florida Keys/Bahamas                  | Greenstein et al., 1998a, b                    |

coral assemblages were subsequently performed on shallow and deep reefs of the Florida Keys by Greenstein and Pandolfi (1997) and Pandolfi and Greenstein (1997b), respectively. These studies revealed complex patterns of fidelity at inter- and intraprovincial scales.

### Comparisons of life, death, and fossil assemblages

The over-arching rationale for coral taphonomic research is a better understanding of the fossil record (Greenstein, 2007). As mentioned above, work on modern coral death assemblages assumes that they provide a reasonable proxy for an eventual fossil assemblage. Comparative studies of coral life, death and fossil assemblages have tested this assumption by including Late Pleistocene (e.g., Greenstein et al., 1998a) or Holocene (Edinger et al., 2001) fossil coral assemblages exposed near localities where modern life and death assemblages are examined. In general, these studies have ascertained that the assumption of a stepwise transition from live to dead to fossil coral reef assemblages is largely false: reef coral death assemblages, generally, are not reasonable proxies for fossil assemblages. Rather, living reefs (i.e., coral colonies that are buried whilst alive) and the death assemblages associated with them apparently are preserved in Pleistocene and Holocene strata.

### Interpretation of depositional environments

A great deal of actualistic (i.e., conducted in modern environments) taphonomic research has revealed the spatial and bathymetric distribution of organisms and physical

environmental processes that leave preservable remains on or in coral skeletal material (see Perry and Hepburn, 2008 for an excellent review). This body of literature shows clearly that “taphonomic signatures” may be used to discriminate between reef subenvironments as well as the history of reef framework accumulation. Such studies are particularly useful for focusing environmental interpretations made from coral material present in cores (e.g., Aronson and Precht, 2001; Blanchon and Perry, 2004). Examination of ecological successions of endo- and epibionts on fossil coral material allowed Perry (2001) to distinguish between layers of reef framework that accumulated via event (storm) deposition from those that represented gradual reef accretion. The refinements in environmental interpretation made in this fashion also have been used to constrain the upper limits of a widely cited Holocene sea level curve (Toscano and Macintyre, 2003) and interpret past incidences of coral mortality events (e.g., Aronson and Precht, 1997; Greenstein et al., 1998a, b; Aronson and Precht, 2001; Hubbard et al., 2005; Aronson et al., 2005).

### Applications to modern reef ecology

Late Pleistocene and Holocene fossil reef coral assemblages are usually exceptionally well preserved (Greenstein and Moffat, 1996; Greer et al., 2009) and contain coral species virtually identical to those living today (Budd et al., 1994). Moreover, Late Pleistocene reefs were thriving during an interval of rapid and dramatic climate fluctuations



(e.g., Pandolfi, 1996). Thus fossil coral assemblages from these time intervals preserve a particularly useful historical record of the response of reef coral communities to an array of ecological and environmental perturbations that occurred in the absence of anthropogenic disturbances. An ever-expanding body of work has sought to establish whether many of the crises affecting modern reefs (e.g., large scale bleaching events, the Caribbean-wide die off of *Acropora cervicornis*, “phase shifts” to alternative reef-dominant taxa) have historic (prehuman) precedents. In numerous studies, Aronson and colleagues (Aronson and Precht, 1997, 2001; Precht and Aronson, 1997; Wapnick et al., 2004; Aronson et al., 2005) have demonstrated that the recent mass mortality of *A. cervicornis* (and in some places its subsequent replacement by a different coral taxon) had no precedent in at least the last 3,800 years in Belize and 1,200 years in Jamaica. Hubbard et al. (2005) described 7,000 years of dominance of the now decimated Caribbean reef crest indicator species *Acropora palmata* in cores obtained from reefs adjacent to St. Croix, US Virgin Islands, although two millennial scale gaps also were identified and attributed to a wider Caribbean phenomenon. Greer et al. (2009) demonstrated the continuous accumulation of *A. cervicornis* over several millennia in Holocene deposits from the Dominican Republic. Examples of coral persistence also have been drawn from Pleistocene deposits in the Caribbean (e.g., Jackson, 1992; Greenstein et al., 1998a) and Indo-Pacific (Pandolfi, 1996) regions. All of these studies point out the stark differences between the historical records of these taxa and their recent declines.

## Conclusion

Studies of taphonomic processes operating in coral reef environments have identified the various mechanisms that serve to remove ecological data from the fossil record. However, much of the literature represents the “information gain” approach to Taphonomy, and has applied taphonomic analyses to refine one’s understanding of the nature of the reef stratigraphic record. Perhaps most important, taphonomic research has underscored the fact that studies of Late Pleistocene and Holocene reef coral paleoecology are essential components of one’s understanding of the crises currently affecting the global reef system.

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## Cross-references

[Binding Organisms](#)  
[Bioerosion](#)  
[Carbonate Budgets and Reef Framework Accumulation](#)  
[Historical Ecology of Coral Reefs](#)

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## TEMPERATURE CHANGE: BLEACHING

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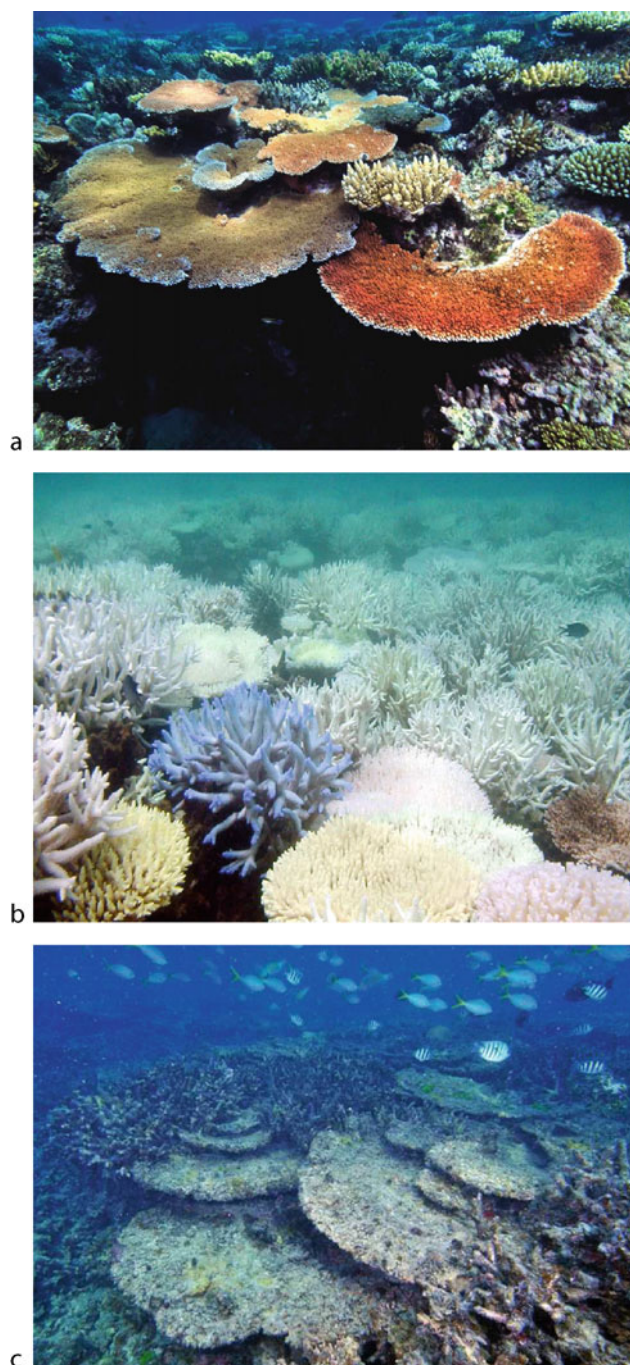
## Definition

Corals respond to thermal stress and synergistic increases in solar irradiance, by whitening or bleaching, a process reflecting the loss of color in symbioses between dinoflagellate algae of the genus *Symbiodinium* and corals.

## Introduction

Sea surface temperatures increased globally by  $0.52 \pm 0.19^\circ\text{C}$  between 1850 and 2004 (Rayner et al., 2006). Based on an earlier dataset, Lough (2004) demonstrated how temperatures had increased by  $+0.17^\circ\text{C}$  over the period 1951–1990 at 16 coral reef sites in the Pacific Ocean, Indian Ocean and Red Sea, an accelerated rate of change not paralleled in the earlier historical record. It has been argued that this ocean warming has moved corals closer to their thermal maxima, with warmer than average years pushing corals over the threshold of thermal tolerance (e.g., Hoegh-Guldberg, 1999). Corals respond to thermal stress and synergistic increases in solar irradiance, by whitening or “bleaching.” Bleaching is the visible sign of the degeneration and/or loss of dinoflagellate symbionts (zooxanthellae), and/or the loss of cells containing these symbionts, from coral tissues as photo-protective mechanisms are lost. The dinoflagellates play a key role in coral metabolism and their reduced function or loss, is accompanied by reduced carbon fixation, coral growth and reproductive ability (Hoegh-Guldberg et al., 2007). There is a perception that bleaching is fundamentally an unnatural phenomenon but symbioses generally display seasonal variation in the density and pigment content of algal cells, with minimal values at the end of the season with the highest sea water temperatures (e.g., Brown et al., 1995; Fagoonee et al., 1999; Fitt et al., 2000); bleaching intensity is an extension of this normal process, with its severity following the length and severity of the warming phase. At the scale of the coral ecosystem, the implications of coral bleaching include significant reductions in the cover of those susceptible species that die *en masse*, changes that occur in community composition and decrease in species and habitat diversity (e.g., Hughes and Connell, 1999). In some circumstances, following mass coral mortality (Figure 1), the dominant benthic cover may switch to a macro-algal community, indicating a phase-shift from a hard to a soft reef (Done, 1992).





**Temperature Change: Bleaching, Figure 1** Appearance of a shallow coral area dominated by *Acropora* corals show that they are (a) normal, (b) bleached, and (c) dead and covered with a low algal community. Photo credits. Australian Institute of Marine Science: (a) and (c) Eric Matson; (b) Ray Berkelmans.

Major coral bleaching events took place in 1982–1983, 1987–1988, 1994–1995 and particularly in 1997–1998 (Figure 2) when, it has been claimed, that 16% of the world's reef-building corals were killed (Walther et al., 2002).

There has been a marked upturn in the record of bleaching events from all the major reef provinces in the 1980s which are difficult to explain solely by improved reporting (Glynn, 1993). One argument, therefore is that the appearance of these impacts represent an early signal of global warming in the oceans, with ENSO triggers to bleaching being superimposed on a secular trend of rising sea-surface temperatures (Figure 3) (Williams and Bunkley-Williams, 1990; Hoegh-Guldberg, 1999).

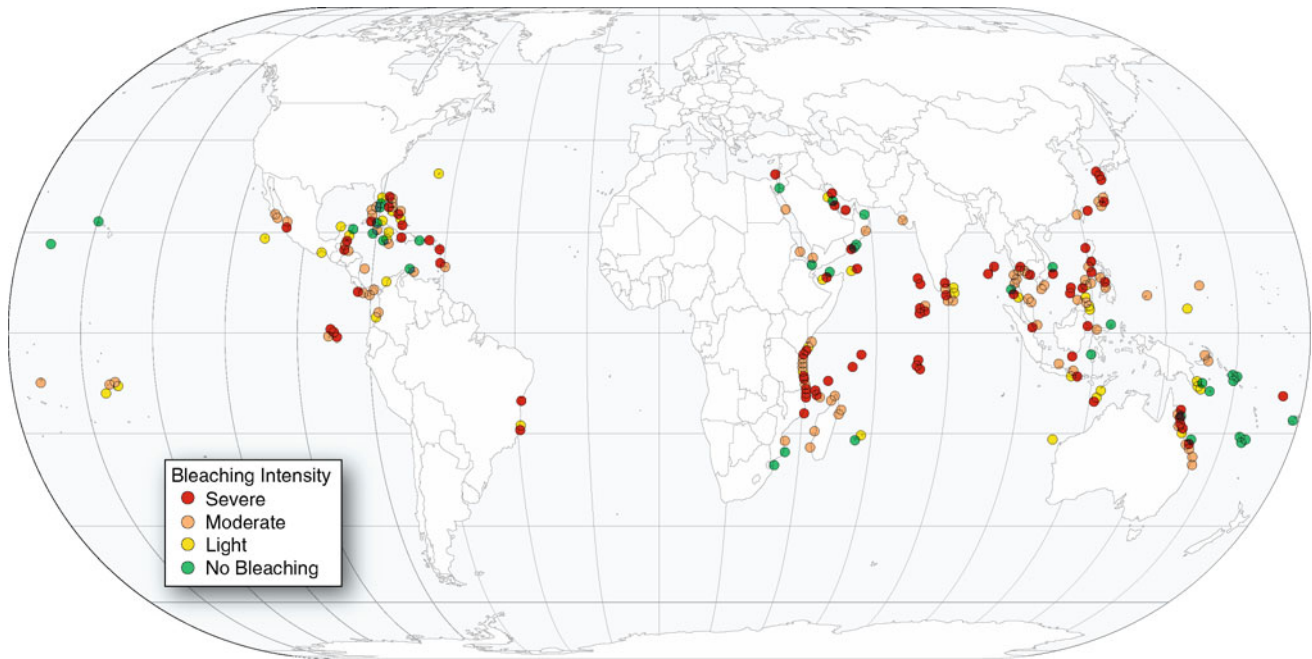
### Geographical patterns of bleaching

Bleaching can be induced by a variety of stressors but thermal stress has been implicated in both local (Figure 4) and large-scale bleaching events (Figure 2) (e.g., Fitt and Warner, 1995; Glynn, 1996; Brown, 1997). The correlation between high sea surface temperature anomalies and bleaching events has enabled the tracking of bleaching hotspots – reef areas where bleaching is likely to occur as a result of temperatures over the usual monthly maxima (Goreau and Hayes, 1994; Strong et al., 1997). In some situations, however, temperature is not an infallible guide to likely bleaching impacts: thus local cloud cover conditions in 1998 in the Society Islands, S.W. Pacific (Mumby et al., 2001) and in Mauritius, W. Indian Ocean (Turner et al., 2000) may have saved these reefs from more severe bleaching impacts at a time of widespread ocean warming. As bleaching is generally correlated with short hot spells rather than mean water temperatures (Berkelmans et al., 2004), the refinement of this approach through the development of indices which look at the time period of heating above a critical thermal threshold, such as Degree Heating Week (DHW; Strong et al., 1997) and Degree Heating Month (DHM), has been effective.

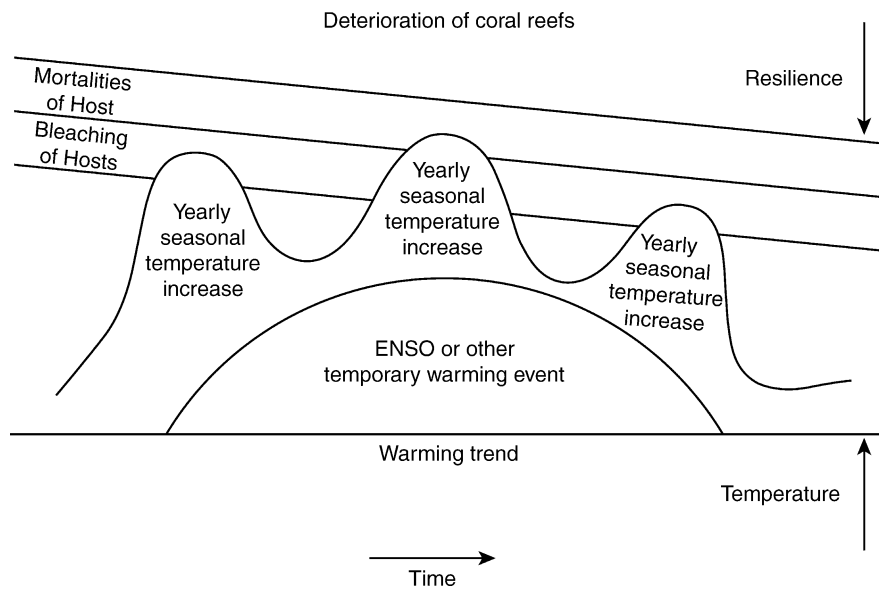
Bleaching associated with up to several weeks of temperature elevations of +1 to +2°C above regional seasonal maxima is often species- and/or reef location-specific and repaired after a few months with little coral mortality. This process is achieved by the repopulation of coral tissues by zooxanthellae that remain in the host. Although numbers may be two to three orders of magnitude less than in healthy corals, bleached corals may nevertheless contain up to 10,000 dinoflagellates cm<sup>-2</sup> (Hoegh-Guldberg and Smith, 1989). However, large temperature excursions of +3 to +4°C, particularly if they are prolonged, can produce mass bleaching of entire reef communities and subsequent coral mortality rates in excess of 90% (e.g., Douglas, 2003; Hoegh-Guldberg et al., 2007).

Whilst satellite temperature is well correlated with field temperature measurements and bleaching incidence when aggregated over space and time, such correlations often break down at the scale of individual reef systems (McClanahan et al., 2007). Indeed, bleaching can be very patchy in time and space, sometimes down to the scale of the individual coral colony. Key environmental factors include light regime (Coles and Jokiel, 1978; Anthony et al., 2007), wave activity (Nakamura and van Woesik, 2001; Nakamura et al., 2003) and thermal microclimates.





**Temperature Change: Bleaching, Figure 2** Global variations in bleaching intensities, 1997–1998 bleaching episode (with permission from UNEP-WCMC).

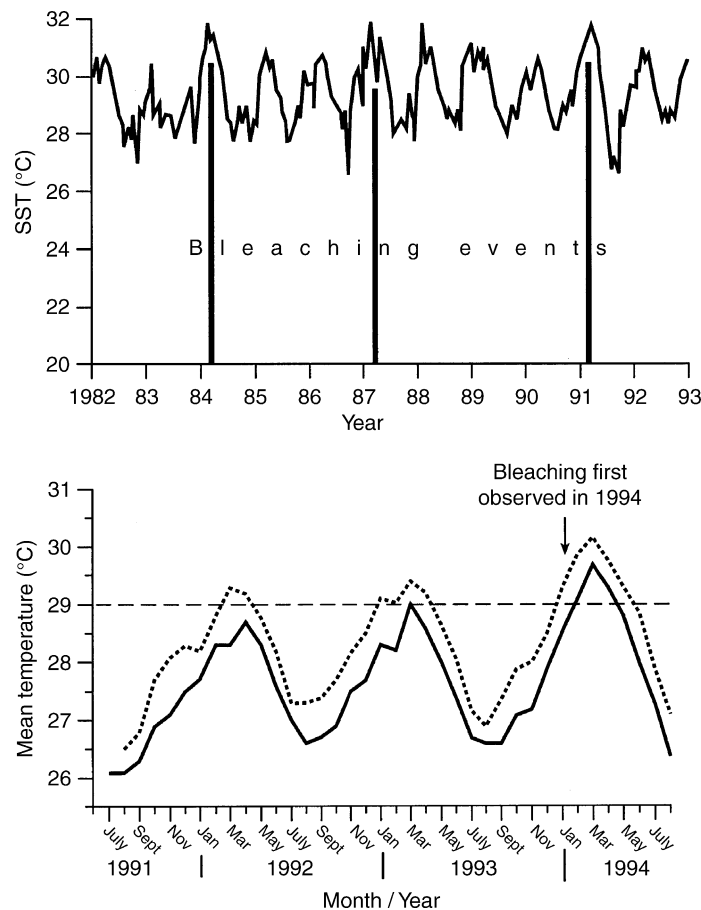


**Temperature Change: Bleaching, Figure 3** Model of the causes of world-wide coral bleaching (after Williams and Bunkley-Williams, 1990).

Local hydrodynamics, in the form of upwelling of cooler deep waters along reef fronts, wave- and tidal-driven current flows on fore-reefs and long water residence times in lagoons with restricted tidal exchange, can all strongly influence patterns of bleaching incidence (e.g., McClanahan et al., 2005), along with variations in water turbidity and variations in coral resilience imposed by differential human impacts.

#### Variability in coral sensitivity to thermal stress

Sensitivity of corals to thermal stress can be highly variable between species (e.g., Gleason, 1993; Brown and Surharsono, 1990; Loya et al., 2001) and even between populations within individual species (e.g., Ulstrup et al., 2006). Thus, for example, during the 1998 bleaching event on the Great Barrier Reef, the hydrocorals (*Millepora* spp.) were the worst affected (85% mortality),

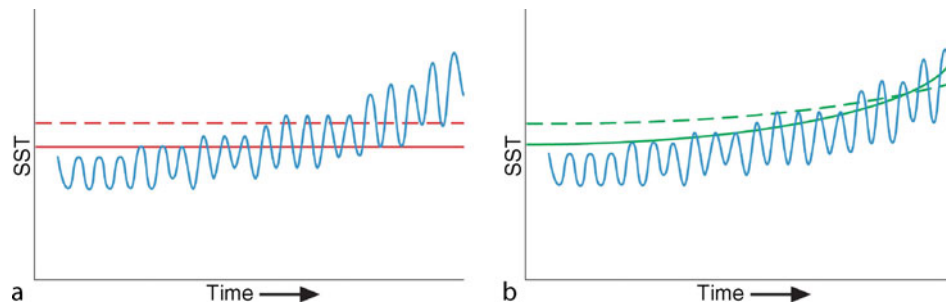


**Temperature Change: Bleaching, Figure 4** (upper) General relations between sea surface temperatures and major bleaching episodes. (lower) Coral bleaching and sea surface temperature, fringing reef, north coast of Moorea, Society Islands, S.W. Pacific Ocean. Temperature measured *in situ* at 14 m water depth; solid line = monthly mean temperature; dotted line = maximum temperature for each month; horizontal dashed line = bleaching threshold temperature of 29°C (after Hoegh-Guldberg and Salvat, 1995).

acroporids and pocilloporids severely affected (18–38% mortality) but poritids and faviids (0–2% mortality) barely impacted at all (Marshall and Baird, 2000).

It is well known that coral populations from warmer waters can withstand higher temperatures compared to populations of the same species that live in cooler waters (e.g., Coles et al., 1976). Furthermore, Berkelmans and Willis (1999) have described the winter thermal limit for *Pocillopora damicornis* on the central Great Barrier Reef as being 1°C lower than the temperature threshold for the same coral species in summer. Developed from these observations is research that suggests that corals, may be able to acclimate (an individual, physiological response) or adapt (a genetic response at the population level) to changed thermal regimes, particularly as a result of shifts in coral host – dinoflagellate relations, creating “new” ecospecies with tougher environmental tolerances and supporting more temperature tolerant strains of zooxanthellae, an idea first put forward by Buddemeier and Fautin

(1993) under the term Adaptive Bleaching Hypothesis. There are several examples of coral hosts containing more than one genetic variety of *Symbiodinium*; and some clades appear correlated with potentially more stressful environmental conditions than others (Rowan et al., 1997). Thus the “type D” symbiont has been shown to confer an additional 1.0–1.5°C tolerance in *Acropora millepora* compared to “type C” (Berkelmans and van Oppen, 2006). In such circumstances, there is likely to be an increase in the thermal threshold to bleaching, a hypothesis supported by field observations which show that past-bleaching episodes can indeed provide corals with some measure of resistance to subsequently raised temperatures (e.g., Brown et al., 2002; Baker et al., 2004). There is potentially a spectrum of coral responses, from the “shuffling” of the relative abundance of symbionts within a coral colony, to the “switching” of symbionts by externally-derived symbionts new to the colony (but not the coral species), to full “evolutionary switching” where



**Temperature Change: Bleaching, Figure 5** Alternative hypotheses concerning the threshold sea surface temperature at which coral bleaching occurs: (a) invariant threshold for coral bleaching = solid line) which occurs when sea surface temperature exceeds usual seasonal maximum threshold (by ca. 1°C) and mortality (dashed line, threshold of 2°C), with local variation due to different coral species or water depth; (b) elevated threshold for bleaching (solid line) and mortality (dashed line) where corals adapt or acclimatize to increased sea surface temperature (from Nicholls et al., 2007, after Hughes et al., 2003).

the host acquires symbionts which have not before been supported by the coral species (Baker, 2001, 2003; Coles and Brown, 2003; Hoegh-Guldberg et al., 2007).

### Summary: Temperature change and coral reef futures

The application of sea surface temperature – bleaching relations to the temperature trends seen in large ocean temperature datasets implies that the threshold temperature at which corals bleach will occur more frequently in the near future, potentially to the point on some reefs where bleaching is an annual event. Such scenarios have been used to drive “time to reef extinction” models (e.g., Hoegh-Guldberg, 1999; Sheppard, 2003). However, not only do the extinction-type models fail to allow for the small-scale patterning of temperature impacts (and thus the possibility of coral survival for re-population within local refugia) but they also fail to take account of the potential adaptive responses of corals and/or their algal symbionts to temperature change (both past and predicted) (Figure 5; Hughes et al., 2003).

It seems more likely, therefore, that the links between coral bleaching and global environmental change will lead to the patchy reorganization of coral communities and the degradation of ecosystem function and diversity rather than complete coral reef loss (Figure 5).

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## Cross-references

[Adaptation](#)

[Climate Change and Coral Reefs](#)

[Corals: Environmental Controls on Growth](#)

[El Niño, La Niña, and ENSO](#)

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## TETHYS OCEAN

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## Definition and introduction

The Tethys was an ancient ocean that existed from 250–~50 million years ago before the evolution of the Indian Ocean. Tethys was orientated east–west and separated the large continents of Gondwana and Laurasia. It was named after the ancient Greek goddess of the sea by Eduard Suess in 1893,

who inferred the presence of a huge ocean using the record of marine fossils from the Alps and Africa.

Many of the Earth's tropical continental shelves at this time were found around the margins of the Tethys Ocean, making the Tethys host to many reef ecosystems for a considerable part of the Mesozoic and into the Cenozoic. At its greatest extent, the Tethys Ocean was part of a continuous series of oceans that covered the Earth between  $\sim 30^\circ\text{N}$  and the Equator, creating circulation patterns quite unlike those known today.

## History

In late Permian times ( $\sim 280$  Ma), the continents were coalesced into one huge landmass known as Pangaea. The C-shaped form of Pangaea enclosed an ocean known as Palaeo- or Neo-Tethys. By the Early Triassic ( $\sim 240$  Ma), an extensive sea-floor spreading ridge (rift) had developed along the northern continental shelf of Southern Pangaea, forming a new ocean along the southern shore of Neo-Tethys. This rift extended from Australia at the southeast corner of Pangaea northwest to the meeting point of the plates of Africa, North America, and Europe. Continued rifting formed an ocean basin bounded to the south and west by the plates of Pangaea and to the north and east by the newly formed microplates of Turkey, Iran, and Tibet. These microplates migrated rapidly northward toward the plates of Eurasia and China, eventually enclosing Neo-Tethys. The Tethys Ocean continued to expand westward, dividing Pangaea into the two large continents of Laurasia in the north and Gondwana in the south, creating an oceanic extension of the Tethys, which today forms the central Atlantic Ocean. Subsequently, the continental shelf known as Cimmeria, traveled north and was, then, subducted beneath the oceanic crust of the Neo-Tethys Ocean under Laurasia, forming the Tethyan Trench. The Mesozoic Tethys Ocean so formed between Cimmeria and Gondwana, over the area occupied by Neo-Tethys.

Between the Jurassic and the Late Cretaceous ( $\sim 100$  Ma), Gondwana began to break up into smaller

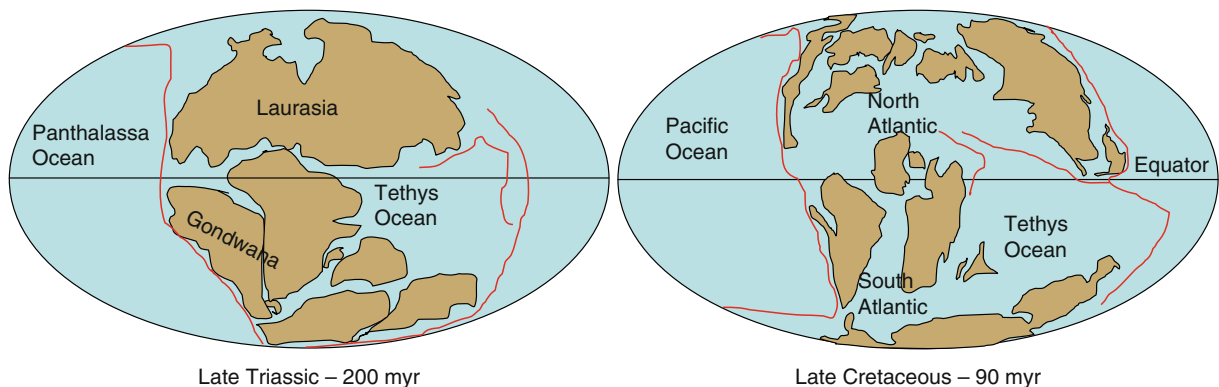
continents, with the Indian and African continents migrating north to create the Indian Ocean (Figure 1). This caused the Tethys Ocean to reduce considerably in area, becoming the Tethys Seaway or the second "Tethys Sea." The Tethys Sea provided a broad marine seaway that connected the Indian and Atlantic oceans until the Miocene.

India, Indonesia, and the Indian Ocean now cover the area once occupied by the Tethys Ocean, and Turkey, Iraq, and Tibet sit on the former continental fragment of Cimmeria. Remnants of the Tethys Ocean include the Mediterranean, Caspian, Aral, and Black Seas (formerly an inland extension of Tethys known as the Paratethys).

## Tethyan reefs

The Tethys was a center of tremendous marine biodiversity, and regional faunal differentiation has been recorded for almost every major period of geological time. Following the end-Permian mass extinction, reef development developed throughout the vast shallow Tethys by the mid-Triassic, in addition to more remote islands in the ancient Pacific, which are now preserved as displaced terranes (a fault-bounded body of rock – sometimes thousands of square kilometers in area – that has been moved from its original position by plate motion). A unique feature found only in the Tethys was the appearance of Permian Lazarus taxa in the Norian, rather than in the preceding Anisian-Ladinian, recovery interval. Late Triassic reefs saw the emergence of scleractinian corals as major reef builders, and this together with a substantial rise in global sea level, allowed for a global expansion of carbonate platforms and high reef biodiversity (Stanley, 1988). Recently, Triassic reefs maximally extended to between  $30^\circ\text{N}$  and  $35^\circ\text{S}$ .

Tethyan reef ecosystems did not show a gradual decline in diversity during the end-Triassic as in other Oceans, but went extinct abruptly at the end of the Triassic. A return to high diversity reefs did not appear until mid-Jurassic time (Stanley, 1988).



**Tethys Ocean, Figure 1** Palaeogeographic reconstructions from the beginning (Late Triassic, 200 million years) toward the end of the Tethys Ocean (Late Cretaceous, 90 million years ago). Red lines mark the major subduction zones. Redrawn from Ron Blakey, NAU Geology.

Even though substantial reefs and carbonates are not common in the Carnian of the western Canadian craton, reef biodiversity was high with more than 50% of known species being also found in Tethys. However, unlike the Tethys, taxa from Norian-Rhaetian terranes are found in lowest Norian rocks. Permian Lazarus taxa are also found in the Norian, and Early Jurassic reefs contain Carnian holdovers, thereby supporting the idea that volcanic islands were refuges in the Panthalassa Ocean during the time when the Tethys Ocean was affected by environmental crises (Stanley, 1988).

During the Jurassic, reefs formed by microbialite, corals, and sponges were widespread along the northwestern margins of Tethys. These reefs occupied shallow- to deep-shelf environments in both pure carbonate and mixed carbonate-siliciclastic settings. Corals were replaced by rudist bivalves in Early Cretaceous reef and carbonate platform communities during a 30 million year period when sea level rose and drowned many continental shelves. Corals appear to have been displaced to the deeper parts of reefs and rudists occupied the shallow, high-energy habitats. By the latest Early Cretaceous, rudists dominated the shallow inner and outer platforms that fringed interior shelf basins, and corals formed reefs together with rudists on the outer shelf margins (Wood, 1999).

After the end-Cretaceous mass extinction, carbonate platforms continued to form on the shores of Tethys. During the Palaeogene, the Earth went through a marked phase of global warming. Between about 60–55 Ma, three stages of carbonate platform development can be identified Tethys-wide (Scheibner and Speijer, 2007). During the first stage, carbonate platforms were populated by corallgal reefs. In the second stage, corallgal reefs thrived only at mid-latitudes and were replaced by larger benthic foraminifera as the dominant carbonate producers in low latitudes. By the early Eocene, newly developed lineages of large foraminifera (“Nummulites”) became the main carbonate-producing biota in low to mid-latitudes. The eventual extinction of the characteristic Palaeo-Mediterranean Nummulite fauna at the end of the Eocene (or in the early Oligocene in eastern Tethys) was apparently accompanied by a global increase in reef coral diversity. The Oligocene represents the height of Cenozoic coral and coralline algal reef development in the western Tethys with maximum abundance, diversity, and cosmopolitan faunas.

## Summary

The Tethys was an ancient east–west ocean that existed from 250 to ~50 million years ago. Many of the Earth’s tropical continental shelves at this time were found around the margins of the Tethys Ocean, making the Tethys host to many reefs for a considerable part of the Mesozoic and into the Cenozoic. The Tethys was a center of tremendous marine biodiversity, and regional faunal differentiation has been recorded for almost every major period of geological time. At its greatest extent, the Tethys Ocean was part of a continuous series of oceans that covered

the Earth between ~30° N and the equator, creating circulation patterns quite unlike those known today.

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## Cross-references

[Foraminifera](#)  
[General Evolution of Carbonate Reefs](#)  
[Plate Tectonics](#)

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## TIDAL EFFECTS ON CORAL REEFS

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## Introduction

The gravitational forces of the moon and sun affect not only the astronomical shelf and ocean surface tides but also force tidal currents on the ebb and flood. The dissipation of energy when tidal currents interact with sea bed, shelf features (coral reefs and *Atolls*) produces friction, vertical shears, turbulence, eddies and transfer of energy to other processes such as internal waves and fronts. This has implication in the vertical and horizontal distribution of temperature and nutrients (*Nutrient Pollution/Eutrophication*) beneficial to coral productivity. Tidal resonance may occur in bays and inlets, forcing tidal features quite unlike the oceanic tides, and hence influence reef exposure, solar insolation and coral desiccation.

## Upper limit of coral reefs

The upper vertical limit of corals, coral sand banks, atoll islands (*Atoll Islands (Motu)*), *Reef Flats*, algae (*Algae*, *Coralline*) and sea grass (*Seagrasses*) development are all dominated by tidal ranges.

With many factors influencing the upper limit of coral growth, it is not possible to relate this to a unique tidal level. A more suitable definition is a range of upper growth limit between Mean Low Water Springs (MLWS) and Mean Low Water Neaps (MLWN), (Scoffin, 1977; Hopley, 1982).

Open water coral reef growth is up to MLWS  $\pm 25$  cm whereas *Microatoll* growth is to MLWN, with *moated* lagoon corals as high as Mean Sea Level (MSL) occurring at Redbill Reef (GBR), as observed by Hopley (1986). The *Moating* of corals on reef flats behind high



*Algal Rims* and cemented *Shingle Ridges* allows reef flat corals to survive extreme low tides (Hopley, 1982).

MLWS is defined as  $Z_0 - (M_2 + S_2)$  and MLWN as  $Z_0 - (M_2 - S_2)$  with Mean Low Water (MLW) =  $Z_0 - M_2$ ,  $M_2$ ,  $S_2$  are the amplitudes of the moon and sun's semi-diurnal harmonic constituents respectively, and  $Z_0$  is MSL (Doodson & Warburg, 1941; Pugh, 1987).

Sea level changes on seasonal and inter-annual timescales are important to the upper limit of coral growth. They need careful identification in tide gauge data and their fluctuations over relatively short periods can be misinterpreted as local rates of sea level rise. For example, in regions of the western Pacific Ocean (within latitudes  $\pm 15^\circ$ ), sea levels dropped by around 30 cm yr during the 1997–8 major El Niño (*El Niño*, *La Niña*, and *ENSO*) and the following year, coming out of *El Niño*, the sea level rose by around 30 cm (Church, et al., 2006). MSL in many tropical regions affected by monsoons has significant seasonal variation; for example, MSL in the *Red Sea And Gulf Of Aqaba* changes 0.5 m between winter and summer monsoons (Admiralty Tide Tables).

Wave heights over reefs will influence the type of dominant coral species with hardy types more resistant to the *Reef Front Wave Energy*. The maximum wave height on a *reef flats* is dependent on water depth and, therefore, on tide level and *Wave Set-Up*, where maximum wave height on a horizontal reef flat is 0.4 (reef flat water depth, see *Reef Flats*) (Sheppard, et al., 2005).

### Coral desiccation and solar insolation

The local time of extreme spring low water is critical to the upper growth of coral reefs i.e., when and how long they are exposed to air and direct UV sunlight, leading to potential desiccation of corals. Corals exposed to air and direct sun for longer than 3 hours, start to wilt and expel the zooxanthella symbiotic algae (Hopley, 1986).

Lowest spring tides occur, when the moon's ( $M_2$ ) and sun's ( $S_2$ ) semidiurnal tides are in phase. As the sun's semi diurnal tide constituent ( $S_2$ ) is fixed to the solar day, so the lowest springs always occur at the same time each day for a location when this  $S_2$  phase is at 180 degrees in the local time (Pugh & Rayner, 1981; Pugh, 1987; Guilcher, 1988).

Time of high water spring tides occurs at  $G * 2$  minutes past midday or midnight (GMT or UT), where  $G$  is the Greenwich phase lag of the  $S_2$  constituent. The low spring tides occur 6 hours before or after this high water time. Phase lag  $G$  can be obtained from harmonic analysis of observed tidal data. GMT can easily be converted to the local time zone. If phase lags 'g' are used in the local time zone, as listed in Admiralty Tide Tables, the same method of determining spring HW and therefore LW is obtained using  $g * 2$ .

Conversion to phase lag  $G$  in GMT/UT from the local time zone phase  $g$  is obtained using  $G = g + \text{zone shift in hours}[\text{west, positive}] \times \sigma$ , where  $t$  is the time zone difference in hours and  $\sigma$  is the angular speed of the relevant constituent (30 degrees per hour for  $S_2$ ) (Pugh, 1987).

For example at Aldabra Atoll, Indian Ocean (*Indian Ocean Reefs*) with time zone GMT + 0300, the oceanic

phase lag  $G$  for  $S_2$  is  $63^\circ$  and  $g$  is  $153^\circ$ . High water springs coincide with  $G * 2 = 126$  minutes past midnight or midday at 14:06 and 02:06 and lowest water springs occurs at 08:06 and 20:06 GMT or 11:06 and 23:06 local zone time.

The Great Barrier Reef exhibits abundant reef flat coral development with lowest spring tides occurring at 14:16 pm at Cairns ( $g$  for  $S_2 = 248^\circ$ ) and 14:38 pm at Heron Island ( $g$  for  $S_2 = 259^\circ$ ). The adjacent Coral Sea reefs have similar times of lowest spring tide.

The tropical seas around Sumatra and Java are dominated by diurnal tides where low tide exposure time for corals is extreme. The dominant  $K_1$  principal solar diurnal harmonic has an angular speed of 15.0411 degrees per hour, so the extreme lowest tides will not occur at the same time of day/night as  $K_1$  advances 4 minutes in 24 hrs.

Tidal predictions, harmonic amplitudes and phase lags are published in most nationally produced tide tables (i.e., NOAA NOS, ANTT-Australia, UKHO). Cotidal charts are useful in visualizing the phase and amplitudes of diurnal or semi diurnal tides in oceans and shelf seas but are difficult to produce in complex coastal waters. The phases of the  $S_2$  harmonic on the cotidal charts are particularly useful in determining the exposure times of corals. For ease of computation and comparison of adjacent seas and time zones the use of phase lag  $G$  in GMT/UT is the convention.

### Diurnal and semi diurnal tides

The distinction between local diurnal and semi diurnal tidal regimes is important in assessment of coral growth, exposure times and desiccation. Diurnal tides dominate in parts of the tropical seas such as around Sumatra, Java and Papua New Guinea. This will significantly prolong exposure times/desiccation of reefs during low water and influence the limit of the upward growth of corals.

The form factor  $F$  (Pugh, 1987; Pugh, 2004) indicates whether local tides are diurnal or semi diurnal and is determined from the ratio of the principle diurnal and semi diurnal harmonic constituent amplitudes, where;

$F = (H_{K1} + H_{O1}) / (H_{M2} + H_{S2})$  and if;  
 $F = 0$  to 0.25 semidiurnal tides dominate,  
 $F = 0.25$  to 1.50 mixed mainly semi diurnal  
 $F = 1.50$  to 3.00 mixed, mainly diurnal  
 $F > 3.00$  diurnal tides dominate.

### Atoll lagoon tidal flushing & residence time

Tidal flows in atoll lagoons (*Lagoons*) are also important in exchanges of water in and out of the narrow entrances.

The twice daily tidal flushing of enriched nutrients (*Nutrient Pollution/Eutrophication*) and organic particulates out of a lagoon benefits nearby outer lagoon corals and fish productivity often seen as oceanic fish shoals feeding at lagoon entrances on ebb tides. The less dense buoyant plume of lagoon water on the ebb tide will feed outer atoll corals/fish in the advection-dispersion mixing process or wind induced longshore current frontal system that can form along the edge of the *atoll* (Wolanski & Hamner, 1988).

The tidal flood of cooler oceanic water helps regulate the temperature and salinity balance in the atoll lagoons which would otherwise increase due to evaporation and solar radiation. Likewise the tidal inflow of oceanic waters avoids eutrophication in the *Lagoons* which would be harmful to lagoon corals and fish.

In atoll lagoons with only narrow entrances such as Diego Garcia and Aldabra (*Indian Ocean Reefs*), tide ranges are reduced and the times of high and low waters are delayed (phase lag) on the oceanic tides (Kjerfve & Knoppers, 1991), which has implications for reef flat upper growth and exposure times.

The practical ratio of minimum inlet(s) channel cross sectional area(s) to the volume of tidal prism within *lagoons* or bays is empirically established as 0.0656 (tidal prism) (Pugh, 2004). If the inlet is narrow or constricted by sand banks, the tidal flow is restricted and the lagoon does not flush, eutrophication occurs with accumulated *nutrients* along with problems of excessive solar heating, leading to mortality of corals.

*Residence Time* for a lagoon can be approximated by (Lagoon depth/Tide range)  $\times$  tidal period (Pugh & Rayner, 1981). The lagoon of Aldabra Atoll, with approximate values for surface area of  $204 \times 10^6 \text{ m}^2$ , volume  $800 \times 10^6 \text{ m}^3$  and depth 4m, has mean spring tide range of 2.78m, (i.e.,  $2(M_2 + S_2)$ ) and neap range of 0.94 m (i.e.,  $2(M_2 - S_2)$ ). This results in residence times of 18 hours (springs) and 53 hours (neaps) for complete lagoon water tidal exchange for a tidal period of 12.42 hours ( $M_2$ ). These times are comparable to Cocos Atoll, Indian Ocean (*Cocos (Keeling) Islands*) (Kench, 1998).

The tide, ebb and flood through lagoon shallow inlets produce plumes of coral sand deposits (Guilcher, 1988) forming sand banks and alluvial fans.

### Tidal distribution of coral eggs/planula

During the annual coral spawning event the fertilized eggs are dispersed by the tides and winds but soon form long surface patches that do not disperse as for normal advection-dispersion in which the width of the patch would normally increase with time (Wolanski & Sarsenski, 1997). During the larvae planula stage of development they are dispersed to the upper surface water column. The residual tidal current vector (difference between ebb and flood) will influence further advection-dispersion (tidal current ellipses have symmetry if ebb and flood vectors equate, otherwise they can be asymmetric and accumulate a residual tidal component over several tidal cycles).

### Tidal stirring/island wakes

Tidal currents can create eddies and wakes in the lee of atolls and reef islands (Wolanski, 1994). Eddies and wakes may only occur during peak tidal currents and only on certain islands/atolls. The turbulence helps in vertical and horizontal mixing of *nutrients*, plankton and temperature from lower stratified layers and benefits to corals.

### Tidal jets

If a series of reefs form a barrier to tidal flows then *Tidal Jets* can form between the reefs. Such an example is seen, along the Ribbon Reef (*Barrier Reef (Ribbon Reef)*) complex off Northern Australia's Great Barrier Reef (*Great Barrier Reef: Origin, Evolution, and Modern Development*). Wolanski, et al. (1988), observed mushroom shaped vortex pair jets on the flood tide helping to sustain the inshore *Halimeda* banks with nutrients. The *nutrients* are upwelled in the strong tidal currents from the lower mixed layer on the outer deeper continental shelf waters. On the flood tide the adjacent corals do not benefit from the nutrient enriched tidal jet. However, on the ebb tide the offshore jet entraps the upwelled nutrients and has benefits for offshore reefs.

### Tidal shelf fronts

The formation of shelf sea fronts (Simpson, 1998) between regions of buoyant stratified water and tidally mixed water has importance in the vertical circulation of *nutrients* from below the pycnocline/thermocline. Simpson and Hunter (1974) developed the relationship between depth ( $h$ ) and tidal velocity ( $u$ ), where if  $\log_{10} (h/u^3) \approx <2$  then mixing by tidal currents will overcome buoyancy. Such large scale fronts do not occur on the Great Barrier Reef but may have significance in other coral populated regions, however limited research is published mostly linked to fisheries. Areas of strong tidal dissipation that can overcome buoyant stratification occur in coral abundant regions in the Andaman Sea, Western Australia (*Western Australian Reefs*) and Sunday Islands, Gulf of Panama, Malacca Strait, Mindanao to N. Guinea and Oman (Hunter and Sharp, 1983). Recent measurements of tidal dissipation by satellite altimetry confirm such regions (Egbert & Ray, 2000).

### Tidal mixing and coral bleaching

Tidal currents in the vicinity of coral reefs are an important source of mixing during periods that lead to Coral Bleaching. These periods are characterised by high insolation, low wind and swell and are known as doldrums in the tropics, when a surface warm layer forms that can cause corals to become heat stressed and expel their symbiotic algae leaving them to look "bleached". The only potential source of cooler waters are from below this layer and mixing by tides can be the critical process that can break down this stable surface layer and spreading the heat throughout the entire water column.

Simpson and Hunter (1974) provide the criterion that can determine whether tidal mixing is strong enough to generate turbulence from the sea floor to reach the surface. Skirving and Steinberg (2003) applied this method utilising a tidal model of the Great Barrier Reef (GBR) by Bode et al. (1997) to generate a mixing map. It also helps explain the complex SST patterns found along the GBR reef matrix and Queensland shelf. A series of studies have been made to determine the applicability to other reef

types such as Scott Reef in the Timor Sea (Bird, 2005) and Palau (Skirving et al., 2010).

The Great Barrier Reef Ocean Observing System (GBROOS) observes these mixing processes in near real time by ocean surface radar and an array of moorings monitoring the stratification and mixing events in the water column (DiMassa et al., 2010).

### Tides in resonance

In bays and long inlets the tide can be in resonance or co-oscillation with the external oceanic or shelf tides, influencing significant changes in tidal range and phase (Bowden, 1983).

An example in tropical coral seas is the *Red Sea And Gulf Of Aqaba*, which exhibits a fundamental co-oscillation with the external tide of the Gulf of Aden. The tide is formed by opposite flows of coastal trapped Kelvin waves which oscillate about the central amphidromic point. The central node or amphidromic point in the middle of the Red Sea between Jeddah and Port Sudan experiences minimal tide and the extreme north and south are in opposite phase in high and low tides (Pugh, 1987).

Spring tidal ranges in the north at Quseir are 0.54 m and south at Gizzan are 0.82 m and middle at Jeddah 0.16 m (from  $2(M_2 + S_2)$ ), but a seasonal MSL variation of 0.5 m dominates with a low in summer and high in winter. Therefore, reef flats may be permanently exposed in the hot summer months in the central region with minimal semi-diurnal tides. At Jeddah, the reef flats are poorly developed for these reasons along with the  $S_2$  tidal phase producing low water springs at 14.30 (Local Time) near the diurnal peak in ambient air temperatures. Hence exposed coral desiccation is extreme in such conditions.

### Internal tides & waves

Internal tides or waves can form on density boundaries in the ocean (e.g. pycnocline) or on the thermocline in oceanic waters and halocline in coastal waters. If their frequency is the same as the surface astronomical tides (barotropic tides), then they are referred to as Internal Tides or Baroclinic Tides when vertical density differences are involved.

Internal waves can also occur at non tidal frequencies. They can all feature wave breaking, internal surf and very large amplitudes, which can influence vertical mixing with implications for coral reefs normally situated in oligotrophic, nutrient low oceanic water. Internal waves can also occur where there is continuous vertical density stratification that is not confined to a simple two layer situation. Here internal waves can travel in all directions and be reflected/refracted off sea bed and shelf, transferring energy throughout.

The principles of internal waves and tides are discussed by Pond and Pickard (1986) and Wolanski, (1994), with a more in depth mathematical approach dealt with by Vlasenko et al. (2005).

Internal waves can be created when the oceanic surface tide wave (barotropic surface tide) passes over an ocean

shelf or around a coral atoll or shallower obstruction such as a seamount. It is then split into a less energetic surface wave and other internal modes with different wavelengths and propagation speeds. This cascading process, from the barotropic surface tides to the baroclinic components, leads to the transformation of tidal energy into turbulence and heat, an important process for the dynamics of the lower ocean (Vlasenko, et al, 2005).

Wolanski and Deleersnijder (1998) and Wolanski et al. (2004) investigated the formation of internal tides/waves around reefs and islands off Western Australia at Scott Reef and at Palau, Micronesia respectively. At Scott reef, strong macro-tidal currents of  $0.6 \text{ ms}^{-1}$  formed internal waves of 60 m peak to trough at diurnal, semi diurnal and higher frequencies.

At Palau, local mixed semi-diurnal surface tides were typically 2 m in amplitude and during spring tides the internal waves exhibited amplitudes of 50–100 m and peaked at 270 m at a range of frequencies including diurnal and semi-diurnal. The implications of such large amplitude internal waves on corals in the region 60–120 m was the rapid temperature change (*Temperature Change: Bleaching*) which was recorded as 8–10°C in an hour and up to 20°C in 30 minutes. The rapid temperature change may stress corals and limit the lower depth of less tolerant species.

From the Scot Reef experiment, observations and modeling results indicate that the 60 m internal waves (peak to trough) cause significant variation in the currents and temperature change in the upper 200 m helping to bring nutrients from below the pycnocline (at 100 m) to 40 m of the surface. Of importance to corals, these nutrient rich waters are then dispersed amongst the spur and grove (*Spurs and Grooves*) structures and surface as observed at the Grand Cayman, Caribbean (Roberts, et al, 1977).

Wang, et al, (2008) used ADCP, CTD and current meters to observe internal waves off Taiwan and clearly describes the vertical profiles of orbital internal tidal ellipses and current vectors, associated with internal waves. The amplitudes of internal wave isotherm displacement observed at over 200 m will influence nutrient mixing and temperature stress on corals.

Katsumata, (2006) observed and modeled internal tides/waves on the Australian North West Shelf, where the energy dissipation of strong tidal currents produce significant vertical stirring and mixing, important for vertical pumping of nutrients.

Energy dissipation occurs when the kinetic and potential energies of a water mass is transformed into other features such as internal waves, eddies, gyres through turbulence and vertical shears encountered with frictional boundaries such as reefs, atolls and sea bed. Significant tidal energy dissipation of the deeper oceans occurs in regions of rough bathymetry such as the *Hawaiian Ridge*, as well as shallow seas and helps in the creation of strong internal tides (Pugh, 1987; Egbert & Ray, 2000; Cartwright, 2001). Internal tides in shelf seas have benefit to coral productivity with vertical mixing of nutrients from below the pycnocline (Wolanski, 1994).



## Tide data

Nationally produced tide table publications (NOAA NOS-USA, ANTT-Australia, UKHO) provide annual tide predictions, constituent phase lags and amplitudes. On remote coral reefs/atolls, there may be limited or no information on tides or local geodetic survey bench marks and may require onsite tide observations and harmonic tidal analysis.

UNESCO's Intergovernmental Oceanographic Commission promotes research quality sea level observations through the Global Sea Level Observing System (GLOSS). Near real time tidal data are accessible from many GLOSS gauges (<http://www.gloss-sealevel.org>). MSL and delayed mode data sets, publications, training material and other resources are available from the Permanent Service for Mean Sea Level (PSMSL) of the International Council for Science (<http://www.pol.ac.uk/psmsl>).

## Summary

The influence of tides on coral reefs is not just confined to the semi-diurnal, rise and fall of sea level. Physical oceanographic studies of coral reefs have investigated the *Great Barrier Reef* where there is ready access and resources that are available for research, with significant research also on Indian Ocean and Pacific coral reefs and atolls. Future coral reef investigations may consider the accumulated literature from the Great Barrier Reef and other much-studied locations in the Pacific and Indian Ocean, with an overall understanding of the interaction of their physical and biological processes.

## Acronyms and abbreviations

ADCP – Acoustic Doppler Current Profiler  
 ANTT – Australian National Tide Tables  
 CTD – Conductivity Temperature Depth  
 GBR – Great Barrier Reef  
 GMT/UT – Greenwich Mean Time or Universal Time  
 NOAA – National Oceanographic Atmospheric Administration  
 NOS – National Ocean Service  
 UKHO – United Kingdom Hydrographic Office  
 UNESCO – United Nations Educational, Scientific and Cultural Organisation

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## Cross-references

Algae, Coralline  
 Algal Rims  
 Atoll Islands (Motu)  
 Atolls  
 El Niño, La Niña, and ENSO  
 Great Barrier Reef Committee  
 Halimeda  
 Hawaiian Emperor Volcanic Chain and Coral Reef History  
 Indian Ocean Reefs  
 Lagoons  
 Microatoll  
 Moating  
 Nutrient Pollution/Eutrophication  
 Red Sea And Gulf Of Aqaba  
 Reef Flats  
 Reef Front Wave Energy  
 Residence Time  
 Seagrasses  
 Shingle Ridges  
 Spurs and Grooves  
 Temperature Change: Bleaching  
 Tidal Jets  
 Upwelling and Coral Reefs  
 Wave Set-Up  
 Western Australian Reefs

## TIDAL JETS

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### Definition

A tidal jet is a fast-moving intrusion of water issuing from a narrow gap through a physical barrier between two bodies of water. The jet is generated by the pressure resulting from height differences between the two water bodies when the surface of one is rising with the tide, but the flow through the channel is too restricted to keep the levels equal. The reverse will occur when the tide is falling.

Tidal jets can occur in coral reef regions when an extensive outer barrier reef is penetrated by only a limited number of narrow channels. Such jets have been studied in considerable detail along the 650 km tract of ribbon reefs between 11 and 16°S on the northern Great Barrier Reef.

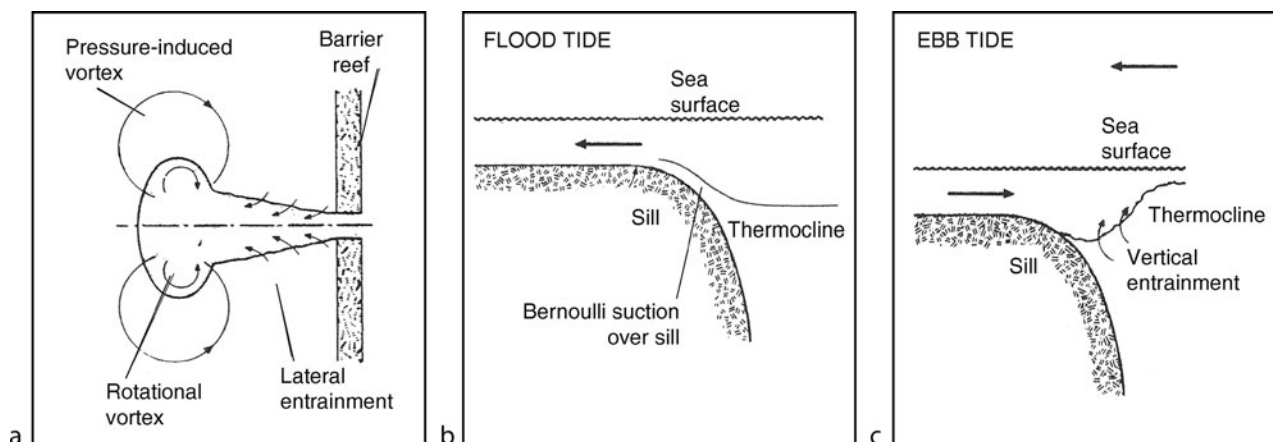
The continental shelf lagoon in that area is 40–50 km wide and the seabed slopes to a depth of 50 m at the outer barrier. Beyond this is the Coral Sea where the continental slope immediately descends steeply, reaching 500 m within 2 km and continuing to at least 1,000 m. The outer barrier is open for only about 10% of its length (Pickard et al., 1977), presenting high resistance to the tidal flow, and causing considerable height differences between the ends of the channels, particularly during spring tides. The resulting strong tidal currents through the channels initially cause a fan-shaped jet to develop, spreading behind the adjacent reefs but, as water velocities increase, this separates completely from behind the reefs to form a distinct mushroom jet capped by rotational vortexes. This jet transports ocean water into the lagoon from beyond the barrier reefs (Figure 1a).

Water in the lagoon and that above the seasonal thermocline in the adjacent ocean, is low in essential nutrients such as nitrogen and phosphorus. However, much greater quantities of these nutrients occur below the thermocline at about 65 m depth in the Coral Sea.

The rapid inflow of water into the channels during rising spring tides can suck water from considerably deeper than the outer channel sill. This process, the Bernoulli Effect, can result in up-welling of cold, nutrient-rich water from below the thermocline. This water is then transported through the channels as a denser bottom layer (Figure 1b), effectively pumping nutrients into the outer lagoon.

Computer modeling indicates that channels 800 m wide, 40–45 m deep at the outer sill and spaced at least 4 km apart can result in significant upwelling from below the thermocline. Many of the channels through the outer barrier meet these criteria (Wolanski et al., 1988).

On the shelf, directly behind the barrier reefs, there is a sparsely colonised sandy strip a few kilometres wide.



**Tidal Jets, Figure 1** (a) Well developed tidal jet and vortex-pair system in plan view; (b and c) vertical sections through the upper continental slope and water column, passing along the axis of the channel. b = flood tide, c = ebb tide.

The seabed then frequently rises rapidly from 50 m up to 30 m depth where extensive meadows of the calcareous green alga *Halimeda* grow atop banks of *Halimeda*-rich gravel. These banks can extend up to 12 km further inshore and cover ca. 2,000 km<sup>2</sup> of seabed (<http://home.austarnet.com.au/research1/atlas/atlas.htm>).

They are situated where the tidal jets decay and deposit their nutrient-rich, up-welled water. The involvement of these nutrients in supporting rich algal growth in the otherwise nutrient-depleted shelf waters is further implied by absence of the *Halimeda* banks behind channels not satisfying the requirements for nutrient upwelling induced by tidal jets (Drew, 2001).

On falling tides, strong currents flow out through the channels, transporting nutrient-depleted water from the shelf. Similar tidal jets develop in the Coral Sea and these can also entrain nutrient-rich water from below the thermocline (Figure 1c). This may explain the considerable growth of phytoplankton visible just beyond the outer barrier on CZCS Satellite imagery.

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## Cross-references

[Halimeda Bioherms](#)  
[Tidal Effects on Coral Reefs](#)  
[Upwelling and Coral Reefs](#)

## TROPICAL CYCLONE/HURRICANE

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## Definition

Tropical cyclone is a generic term that also includes hurricane and typhoon. Meteorologists define a tropical cyclone as "... a non-frontal low pressure system of synoptic scale developing over warm waters having organized convection and a maximum mean wind speed of 34 knots (70 km h<sup>-1</sup>) or greater extending more than half-way around near the center and persisting for at least 6 h" (BOM, 2009).

In the Northern Hemisphere, tropical cyclones rotate in an anticlockwise direction. They are referred to as *hurricanes* (North Atlantic, North East Pacific east of the dateline), or *typhoons* (Northwest Pacific east of the dateline). In the Southern Hemisphere, they rotate in a clockwise direction, and are called *cyclones* in the Indian Ocean and the Pacific Ocean west of 160°E, and *hurricanes* east of 160°E.

Tropical cyclones have a distinctive "eye," which is usually some tens of kilometers across, and a surrounding cloud mass that is some hundreds of kilometers across. Unlike *tornadoes*, which are an order of magnitude smaller and generated on and move across land, tropical cyclones are generated only at sea.



## Introduction

Cyclones are a normal part of the marine and coastal environment in the latitudinal bands 7–25° north and south of the equator – about 70% of the tropical seas in which coral reefs occur. Affected reefs are exposed to one or more of four potential impacts: powerful short period waves generated in chaotic seas generated by winds spiralling in toward the eye; swells (high, long period waves) that break onto reefs at great distances from the eye; storm-surges (elevated sea levels – a direct consequence of the low-pressure cell), and flooding rains (either directly or in river plumes).

In a major review, Scoffin (1993) listed the following reef areas as regularly exposed to cyclone impacts: north-west Pacific Ocean from the Marshalls and Marianas to the Caroline Islands, South China Sea, and the Philippines; southwest Pacific Ocean from Society, Cook, and Samoan Islands, Tuvalu, to Fiji, Vanuatu, New Caledonia, and the Great Barrier Reef of Australia; the north Indian Ocean, including the Andaman Islands, Sri Lanka, and the Lakshwadeep islands; south Indian Ocean, Cocos Keeling, Chagos Archipelago, and the islands between Madagascar and the Mascarenes; the northwest Atlantic Ocean including the Gulf of Mexico and the Caribbean Sea.

By contrast, equatorial reefs (to latitudes ~7° north and south) – notably including most of those in the Coral Triangle (see entry *East Indies Triangle of Biodiversity*) – are rarely if ever exposed to such extreme environmental impacts as those generated by cyclones. These areas are the Maldives; the East African coast; the Red Sea; the area from the Malaysian peninsula through northern Indonesia, Papua New Guinea, and the Solomon Islands; the Pacific atolls of Kiribati, the Phoenix group, many of the Line Islands, and the easternmost Tuamotus (Scoffin, 1993).

## Cyclone genesis

Cyclones are generated and maintained over the ocean by a combination of meteorological and oceanographic conditions and processes that rarely occur nearer than 500 km from the equator: a “heat engine” (warm waters ( $\geq 26.5^\circ\text{C}$ ) to ~50 m depth or more); a cool, moist atmosphere with weak vertical wind gradients that draws heat from the ocean heat engine to generate thunder storms; sufficient Coriolis forces to maintain the low-pressure cell; a pre-existing weakly organized rotating weather system (BOM, 2009). Such conditions occur every summer, generating cyclones that move across the ocean at speeds of 10–25 km h<sup>-1</sup>. The average wind speed at 30–50 km radius around the eye’s center ranges from 62 to 244 km h<sup>-1</sup> (gusting to 88–344 km h<sup>-1</sup>, Table 1), creating destructive waves as highly turbulent wind energy is transmitted to the water surface. The net movement of these wind waves is in the direction of the wind flow (Massel, 1999). Since a cyclone’s wind flow is rotating, it can drive powerful waves into parts of reefs that are normally highly sheltered from the prevailing fair weather waves and whose corals and reef matrix are ill-adapted to withstand strong wave action. When the eye is in motion, wind speeds and waves are larger on one side of the track than the other (as the forward motion is added or subtracted to the rotational speed). There is, for example, a 50-km h<sup>-1</sup> difference in wind speed to the left and right of the track of a cyclone moving at 25 km h<sup>-1</sup>, with concomitant differences in the waves they generate.

## Waves and currents

Hearn (1999) and Massel (1999) provide general accounts of waves in coral reef environments. As a wave approaches

**Tropical Cyclone/Hurricane, Table 1** Comparison of the USA hurricane scale with the Australia’s tropical cyclone categories. The demarcation points are not precise – this table is intended to provide a rough comparison only. ([http://www.bom.gov.au/weather/wa/cyclone/about/faq/faq\\_def\\_2.shtml](http://www.bom.gov.au/weather/wa/cyclone/about/faq/faq_def_2.shtml))

| USA category | Australian category | Approximate central pressure (hPa) | 1-min av. wind speed (knots) | 10-min av. wind speed (knots) | Wind gusts (knots) | Wind gusts (km/h) |     |
|--------------|---------------------|------------------------------------|------------------------------|-------------------------------|--------------------|-------------------|-----|
| Category 1   | Category 1          | >985                               | 39                           | 34                            | 48                 | 88                |     |
|              | Category 2          | 985–970                            | 65                           | 57                            | 81                 | 149               |     |
|              |                     |                                    | 70                           | 62                            | 87                 | 161               |     |
| Category 2   | Category 3          | 970–955                            | 75                           | 66                            | 93                 | 172               |     |
|              |                     |                                    | 80                           | 70                            | 99                 | 184               |     |
|              |                     |                                    | 85                           | 75                            | 105                | 195               |     |
|              |                     |                                    | 90                           | 79                            | 112                | 207               |     |
| Category 3   | Category 4          | 955–930                            | 95                           | 84                            | 118                | 218               |     |
|              |                     |                                    | 100                          | 88                            | 124                | 230               |     |
|              |                     |                                    | 105                          | 92                            | 130                | 240               |     |
| Category 4   |                     |                                    | 110                          | 97                            | 136                | 253               |     |
|              |                     |                                    | 115                          | 101                           | 143                | 264               |     |
|              |                     |                                    | 120                          | 106                           | 149                | 275               |     |
| Category 5   | Category 5          | <930                               | 125                          | 110                           | 155                | 287               |     |
|              |                     |                                    | 130                          | 114                           | 161                | 298               |     |
|              |                     |                                    | 135                          | 119                           | 168                | 310               |     |
|              |                     |                                    |                              | 140                           | 123                | 174               | 321 |
|              |                     |                                    |                              | 145                           | 128                | 180               | 333 |
|              |                     |                                    |                              | 150                           | 132                | 186               | 344 |

a gently sloping reef, it accelerates across the reef slope and breaks on its shallows. Compared to normal fair-weather waves, a cyclone-generated wave introduces strong hydraulic conditions into reef zones and habitats usually exposed to more moderate forces. Bigger than normal waves, especially if coincident with a low tide, introduce strong water motion deeper down the slope than its normal fair-weather depth. A storm surge, especially on top of a high tide, causes the breaker zone to move toward the back reef, relative to its normal fair-weather position. In each case, the anomalously high forces impact upon reef components (corals; framework) that developed in calmer conditions and are structurally ill-adapted to the extreme high forces. Beneath the wave's surface expression, the upward component of oscillatory water motion exerts lift forces on the underside of horizontal projections from the reef (corals; framework), horizontal components undercut them, and the downward component exerts percussive impacts.

### Hindcasting winds, waves, and coral damage

Cyclones routinely travel for hundreds to thousands of kilometers at 10–25 km h<sup>-1</sup>, sometimes pausing along the way. Kjverfve et al. (1986) provided functions to hindcast the progressive changes in local wind speed and wave characteristics (significant wave height; period) at a single reef site (Discovery Bay, Jamaica) as a hurricane passed 50 km to its north. Done (1992) applied an extension of this approach to estimate local wind speeds, duration, and direction of attack as a proxy for wave impact and predictor of damage at a large number of sites at varying distances (0–160 km) from the path of a cyclone that crossed the Great Barrier Reef, Australia. Massel and Done (1993) and Madin and Connelly (2006) quantified the relationship between wave energy and the breakage or dislodgement of coral of different sizes, shape, and tenacity of attachment. Massel and Done (1993) produced survivorship curves for unattached head corals at different locations and depths on a reef, factoring in the attenuation of wave energy with depth, coral growth rates, and the meteorological record of cyclone frequency and intensity.

### Cyclone effects on coral reefs

The repetition of short-period wave impacts hundreds to thousands of times over periods of several hours causes major coral mortality and structural damage to reefs. (By contrast, any single tsunami's damaging affects are due to the actions of a very small number of extremely powerful waves – see entry *Tsunami*). Impacts on the reef include not only the direct effects of wave damage (e.g., coral breakage and dislodgement; horizontal movement of debris; Done, 1992; Scoffin, 1993; Fabricius et al., 2008), but also burial and breakage cause by the avalanche of reef and coral debris down reef slopes (Harmelin-Vivien and Laboute, 1986). While cyclone damage to corals is indisputable, Massel and Done (1993) and Madin and Connelly (2006) concluded that the damage is not caused by wave forces *per se*. These are insufficient to break

massive or branching corals which are securely attached to solid reef platform. However, the point of attachment is frequently insecure, and the object to which it is attached is often not solid reef platform (e.g., fragile and eroded framework, coral skeletons, coral rubble, or mollusc shells). Such corals can be swept, rolled, and pushed across the reef, damaging or destroying them and other corals and topographic high-spots with which they collide.

Recurrent attack by strong breaking and surging waves can undercut shallow reef framework and cause it to collapse; it can fracture and disintegrate slabs of reef framework meters across and >100 tons in weight, throwing them intact onto the adjacent reef flat (Scheffers and Scheffers, 2006). Over a period of hours, surging reef top currents move such boulders tens to hundreds of meters by overturning (rolling) and sliding (skidding) (Scheffers and Scheffers 2006; Goto et al. 2009). The latter authors estimated the characteristics of the cyclonic waves necessary to put massive reef blocks in observed reef-flat positions: at 30 m from the reef edge, a significant wave height of 4.2 m and current velocity of 6.5 m s<sup>-1</sup>; at 260 m from the edge, 1.5 m and 3.1 m s<sup>-1</sup>. These are extraordinarily large waves and strong currents compared to fair-weather conditions, wherein values one-third of these would be normal for equivalent places. In some settings open to long ocean fetches, the initial upward displacement of rubble beds and very large coral heads or reef blocks may have been made by a tsunami (Nott 1997; Scheffers and Scheffers, 2006; see also entry *Tsunami*).

Cyclonic waves can set up extraordinarily strong currents across a reef flat. Working in concert with existing geostrophic and tidal currents, jets, and eddies, these currents move sand, shingle, and small debris *en masse* into new reef flat or onshore positions, the final location depending in part on the sea level relative to the reef top (Hearn, 1999) and the state of the tide during the cyclone's passage (Scoffin, 1993). Extreme storms create, move, or destroy sand or shingle cays (Scoffin, 1993) and deposit what soon becomes discrete habitat with distinctive biota (e.g., reef-flat boulder zones and shingle beaches, both of which are derived from broken and dislodged corals). Gravel, rubble, blocks, and corals are propelled through the water, rolled, and skidded across the reef to lower energy deposition sites, be they talus beds at the base of reef slopes, reef-flat boulder ramparts, sheltered back-reef lagoons, or the slopes or floors of channels through or between reefs. In transit, entrained rubble and corals smash against other corals, causing breakage and injury to both entrained and attached corals (Done, 1992; Scheffers and Scheffers, 2006). Wholesale movement of thousands of tons of sand, gravel, and rubble can eliminate or shift an entire sand cay, bury thriving coral assemblages, expose formerly buried substrata, raise the height of the intertidal reef flat, add to an adjacent shoreline, and modify reef-top draining, as channels are opened up and occluded. On the reef flat during the actual passage of the cyclone, as Scoffin (1993) suggests, processes of deposition will predominate during low tide, and the

processes of erosion during high tide. The final geological signature of a particular event at a particular reef may thus be greatly influenced by the state of the tide at the time cyclonic conditions subsided.

### After the cyclone

In the weeks to decades that follow a serious impact, changed reef-top hydrodynamics may be to the benefit of coral-dominated ecological assemblages (deeper and better flushed areas more accessible to colonizing organisms), or to their detriment (when loss of circulation causes deleterious changes in temperature, salinity, oxygenation, and turbidity – Macintyre, 2007). The freshly dead skeletons, rubble, and denuded framework in previously coral-dominated areas will be colonized by a succession of microbes, cyanobacteria, and algae. In poorly flushed areas, this benthic shift may be at the expense of any potential coral recolonization; in well flushed areas, it may be a step in a succession to encrusting coralline algae and eventual dominance by corals. In the latter circumstances, periodic disturbance can help maintain coral and coral-dependent species diversity in the long term (Connell, 1978; Bythell et al., 2000; Woodley, 1992; Done et al., 2007).

### Contrasting perspectives on tropical cyclones

From an ecological perspective, the damage to a particular part of a reef (breakage, dislodgement and death of coral colonies) may be minor (requiring only months to years for coral populations and dependent biodiversity to recover) to catastrophic (years to decades). Indeed, by transporting viable coral fragments, a storm can initiate the re-population of previously barren areas, newly devastated areas that the storm itself created, or previously buried substratum that the cyclone exposed. From a geological perspective, the generation of new sediments (coral breakage) or the movement of existing deposits caused by a single cyclone may represent anything from a minor blip to a major transformation of the reef that will be preserved in its structure for millennia (Scoffin 1993; Scheffers et al., 2009). Though a given cyclone may be highly damaging to corals and reef framework, in some settings, the coral regeneration, amalgamation, and infilling initiated by the event can cause reefs to extend laterally by “stepping out over their own debris” (Blanchon and Jones, 1997).

At a regional scale, the historical cyclone regime (the frequency and extent to which coral populations are decimated, incipient reef structures are smashed, inundated by flood waters, or smothered in silt) may also be reflected in both ecology and geology. Ecologically, the specific regime can affect the rate of population turnover and the size structures of important reef building corals (Done, 1992; Massel and Done, 1993; Madin and Connelly, 2006); geologically, it can determine the ability of reef growth to “keep up” during periods of rapid sea-level rise and horizontal transgression of the sea across coastal lands (Macintyre, 2007; Larcombe and Carter, 2004). Indeed, the latter authors explain the absence of reefs

from large parts of the central Great Barrier Reef that were first inundated ~7 ky BP in these terms.

Systematic variation in the extent of development of buttresses and the types of dominant corals around very large reefs can be largely understood in terms of differences in the relative importance of hurricane impacts. These in turn depend to a great extent on the length of open ocean (*fetch*) to seaward of the section of reef in question. At Grand Cayman, for example, differences in buttress development are explained in terms of differences in the fetch and, thus, in the importance of hurricane-induced pruning of branching corals and the flushing of sand through canyons by return flows (Blanchon and Jones, 1997).

### Summary

Cyclones often leave broad swathes of damage to coral reefs, with significant ecological and geological outcomes. The rotating structure of any single cyclone can cause structural damage and sediment transport in areas that are normally sheltered, initiating a period of ecological regeneration within physical and environmental settings that may be quite different from those present before the storm.

Considered in the context of the Holocene period of transgression and reef development, a local cyclone regime that is too severe (in terms of frequency, intensity) may exclude coral reefs from some areas. Where the regime is more moderate, cyclones can be formative events in terms of both ecology (initiating a period of regeneration) and geomorphology (building islands; transforming reef-top morphology; facilitating lateral reef extension onto the adjacent shallow sea floor). With twenty-first century climate change, projected reduction in the reef-building performance of corals and increased severity and/or frequency of cyclone impacts have implications that are potentially important but as yet poorly understood (see entry *Climate Change: Increasing Storm Activity*).

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## Cross-references

[Corals: Environmental Controls on Growth](#)  
[Climate Change: Increasing Storm Activity](#)  
[Ocean Acidification, Effects on Calcification](#)  
[East Indies Triangle of Biodiversity](#)  
[Tsunami](#)

## TSUNAMI

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## Definition

*Tsunami* refers to a fast moving wave or series of waves caused by rapid displacement of a large volume of ocean water. These gravitational oscillations of the entire water body of an ocean basin possess large wave lengths (~300 km), long periods (typically 10 min to hours), and travel at great speeds across ocean basins (~220 m s<sup>-1</sup>).

## Introduction

The term tsunami is derived from the Japanese language, and literally translated it means “harbor” (*tsu*), “wave” (*ami*). More than 195 tsunami have been recorded along the Japanese coast. Despite the limited spatial extent of waves implied by this name, the term has been adopted in the scientific literature to describe the fast moving trans-oceanic wave events that have the potential to cause mass devastation.

On human timescales, devastating tsunami are a relatively rare occurrence, but the consequences of exposure to such events can be immense. Over the past century, more than 1,040 tsunami have been recorded (Scheffers and Kellett, 2003). However, the majority of these events have been low in magnitude with negligible impacts. Disastrous events, with flow depths at the coast of >10 m, constitute only about 2% of the centennial tsunami record.

On a geological timescale, tsunami are regular occurrences. Global tsunami catalogs indicate there have been more than 2,000 tsunami events during the past 4,000 years (NGDC, 2009), although this value is likely an underestimate due to the lack of early records. Coral reefs and reef-associated sedimentary landforms occur throughout the Caribbean Sea and tropical Indian and Pacific Oceans. These reef systems are surrounded by tsunamigenic seismic zones and have been subjected to multiple tsunami during the Holocene. Indeed, these ocean basins account for 75% of all tsunami. While much attention has focused on the role of extreme storms and cyclones in promoting change in coral reef ecosystems (Woodley et al., 1981; Connell et al., 1997; Done, 1992a, b; Woodley, 1992) and geomorphic structure of reef systems (Stoddart, 1963; Maragos et al., 1973; Bayliss-Smith, 1988; Scoffin, 1993; Blanchon et al., 1997), until recently little was known of the direct impact and long-term consequences of tsunami on coral reef ecosystems and associated reef landforms.

The Sumatran tsunami in 2004 was the worst tsunami disaster in recorded history. This event provided a significant impetus for research on the impacts of tsunami on ecosystems, landforms, and human communities. Of note, the event provided the first mega-tsunami with which scientists could document impacts on coral reefs, and against which they could calibrate historical reconstructions of tsunami impact.

The focus of this entry is to examine the causes and characteristics of tsunami, their interaction with reef structures and their ecological, geological, and geomorphic impacts on coral reef systems.

## Mechanisms of tsunami generation

When a major Chilean earthquake generated a Pacific-wide tsunami in 1964, little was known of the mechanisms controlling tsunami generation (Satake et al., 2007). However, subsequent scientific breakthroughs in plate tectonic theory, coupled with development of numerical models and seismic monitoring, have considerably increased scientific understanding.

Earthquakes are the most common cause of tsunami. They can cause faulting and deformation of the ocean floor that displaces large volumes of ocean water that trigger tsunami waves. Tsunami genesis is thus dependent on the location and magnitude of the seismic event and the extent of displacement of the sea bed. Earthquake sources are located deep beneath the earth surface, and since their coupling with the ocean is weak, small earthquakes generally do not generate tsunami of any consequence. It is the larger earthquakes (moment magnitude  $>8.7$ ) that generate the largest tsunami waves (Okal, 2009).

Submarine mass failure (underwater slides or slumps) or aerial landslides (sometimes triggered by lesser earthquakes) can also trigger tsunami. For example, the tsunami that impacted the northern shoreline of Papua New Guinea in 1998 resulted from a submarine mass failure triggered by a magnitude 7.1 earthquake along the boundary of the Australian and Pacific plates (Synolakis et al., 2002). Similar earthquake-triggered submarine failures have been implicated in generation of a tsunami in 1992 at Flores, Indonesia (Imamura et al., 1995), and one that inundated Hilo, Hawaii in 1946, following an earthquake near the Aleutian Islands, Alaska.

There are also non-earthquake triggers for tsunami, notably volcanoes and bolides. Large-scale volcanic eruptions in the marine environment that have generated tsunami in recent history include those of Krakatau (AD 1883) and Santorini (1630 BC). Ocean bolide impacts, while infrequent in the geological record, have the potential to generate massive tsunami, as has been inferred in the Yucatan 65 million years ago (Bryant, 2008).

Tsunami are generally categorized based on the geographic reach of their influence relative to their point of origin. Commonly, locations in close proximity to the seismic source (within 1,000 km) are considered to be in the “near-field.” Sites beyond this threshold are considered to be in the “far-field.” However, Titov et al. (2005) challenged this distinction based on the global reach of the Indian Ocean tsunami suggesting that all coastlines in the Indian Ocean basin were in the “near-field.”

### Characteristics of tsunami waves

Tsunami are characterized by wave lengths up to and in excess of 300 km, long wave periods of 10–60 min and propagation speeds up to  $800 \text{ km h}^{-1}$ . In the deep ocean, tsunami waves typically have low amplitude ( $<1 \text{ m}$ ). These parameters are in marked contrast to those of wind-generated waves, which are characterized by shorter wave lengths (typically  $\leq 0.2 \text{ km}$ ), shorter periods (3–30 s), slower propagation speeds ( $54 \text{ km h}^{-1}$ ), and greater wave heights (up to  $\sim 12 \text{ m}$ ). Another critical difference between tsunami and wind-generated waves is the location of energy within the wave, and how it is conveyed across the ocean. Wind-generated wave energy is transferred across the ocean surface, and there is no translatory flow of water until the wave comes close to the break point. The energy in the wave is mostly contained

near the surface, decaying exponentially to a negligible level by a depth of one half the wave length. In contrast, tsunami waves are much longer and energy is distributed throughout the entire water column. Moreover, there is substantial horizontal movement of the water body itself across the ocean (Yeh et al., 1994).

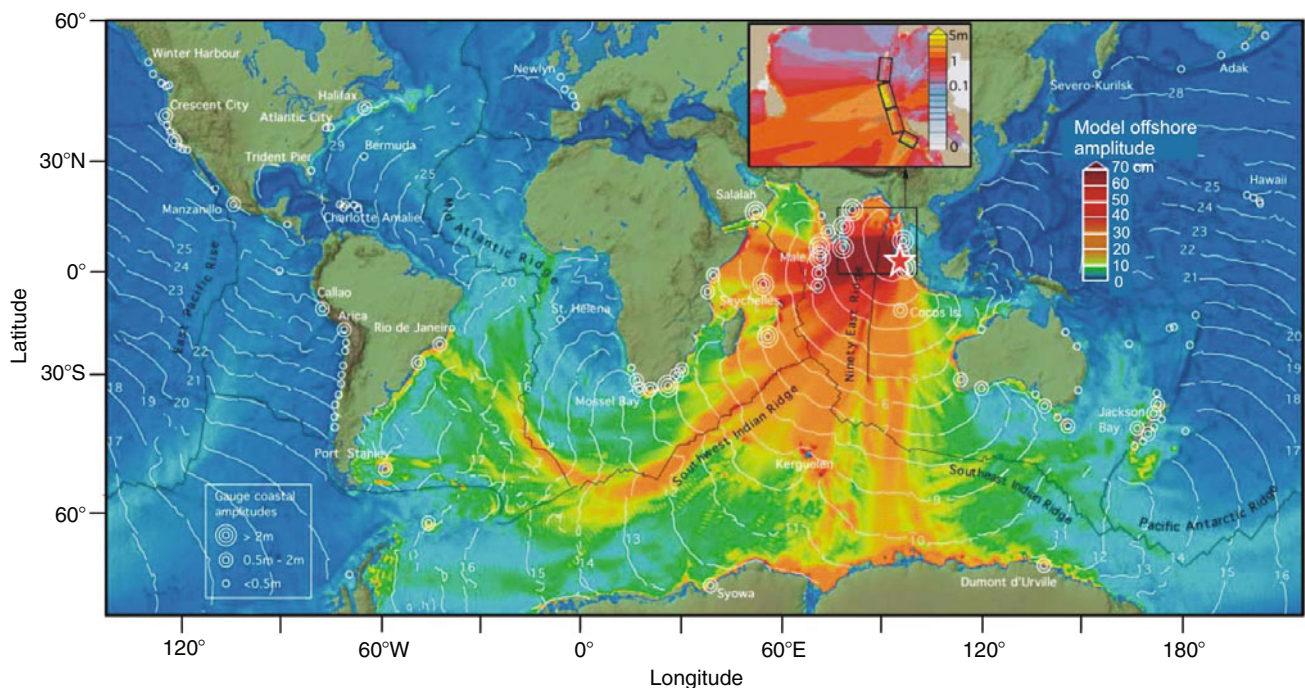
The generation mechanism of tsunami waves controls both their local character and their geographic reach. Earthquakes can move extremely large volumes of water as a consequence of the significant length of rupture zones ( $\sim 10^3 \text{ km}$ ), although the water column is moved vertically by only a small distance ( $\sim 10^0\text{--}10^1 \text{ m}$  in the largest quakes). For example, the Sumatran tsunami of 26 December 2004 was generated by a fault rupture that extended 1,200 km with sea floor displacement of approximately 20 m (Stein and Okal, 2005). This produced very long waves that possessed large amounts of energy and that were transmitted large distances with minimal energy loss (e.g., Figure 1). Non-earthquake sources (e.g., submarine failure), by contrast, typically displace water across a smaller linear distance ( $\sim 10^1\text{--}10^2 \text{ km}$ ) and move smaller volumes of water. The resulting tsunami waves have shorter wave lengths and undergo more efficient dispersion, losing energy during propagation, and have more limited geographic reach (Synolakis et al., 2002).

Tsunami events commonly comprise a series of large waves at intervals up to 60 min. For example, tide gauges from the eastern and central Indian Ocean show a number of large waves following the Sumatran earthquake with water-level oscillations continuing for more than 24 h (Figure 2).

### Tsunami wave propagation

Tsunami wave height, directionality, and propagation patterns are controlled by the orientation and intensity of seismic line sources and trapping by mid-ocean ridges (Titov et al. 2005). Ocean ridges guide the direction of wave propagation (Figure 1). Consequently, ocean bathymetry has a significant control on tsunami propagation behavior.

Although the height of tsunami waves in the open ocean is generally small ( $<5 \text{ m}$ ), they can shoal markedly close to the coast and produce wave run-up depths on the order of 10–100 m (Bryant, 2008; NGDC, 2009). As waves enter shallow water they are transformed, reducing in speed and increasing in height. The degree of shoaling and final interaction of tsunami waves with reefs and shorelines is dependent on the nearshore bathymetry and planform shape of reefs. In general, shoaling is most efficient and produces largest wave heights on low gradient and shallow coastal shelves (Okal, 2009). Spatial differences in bathymetry, therefore, is one of the major controls on the transformation of tsunami waves and their consequent impacts on coral reefs and reef-associated landforms (Ioualalen et al., 2007; Scheffers et al., 2009). For example, while the mid-ocean height of the Sumatran tsunami was mostly  $<0.7 \text{ m}$ , maximum wave height, near the coast at Banda Aceh was estimated at 10–15 m (Spencer, 2007).



**Tsunami, Figure 1** Global reach of the December 2004 Sumatra tsunami. Colors show maximum computed tsunami heights during 44 h of wave propagation simulation. Contours show computed arrival time of tsunami waves. Circles denote the locations and amplitudes of tsunami waves in three range categories for selected tide-gauge stations (From Titov et al., 2005).

### Interaction of tsunami with coral reefs

The interaction between tsunami waves and coral reefs occurs at a number of spatial scales. The nature of these interactions influences tsunami wave propagation, the specific transformation of tsunami waves, and the way in which tsunami wave energy is released on reef structures and associated reef landforms.

#### Macro-scale influence of reef systems on transoceanic tsunami behavior

Mid-ocean archipelagos and shelf reef systems (barrier reef complexes) present a physical barrier to tsunami waves, modifying their transoceanic propagation in a number of ways. First, the interaction absorbs energy from tsunami. For instance, during the Sumatran tsunami, the tsunami's interaction with the Laccadive – Maldives – Chagos ridge and atoll system reduced its height by as much as 0.3 m (Figure 1). Second, it can deflect tsunami energy into otherwise “sheltered” coastal sites, and alter the overall direction of the tsunami's propagation. For example, reflected waves from the Maldives have been implicated in the destruction on the southwest coast of Sri Lanka (Liu et al., 2005; Kowlaik et al., 2007).

#### Reef platform – tsunami interactions

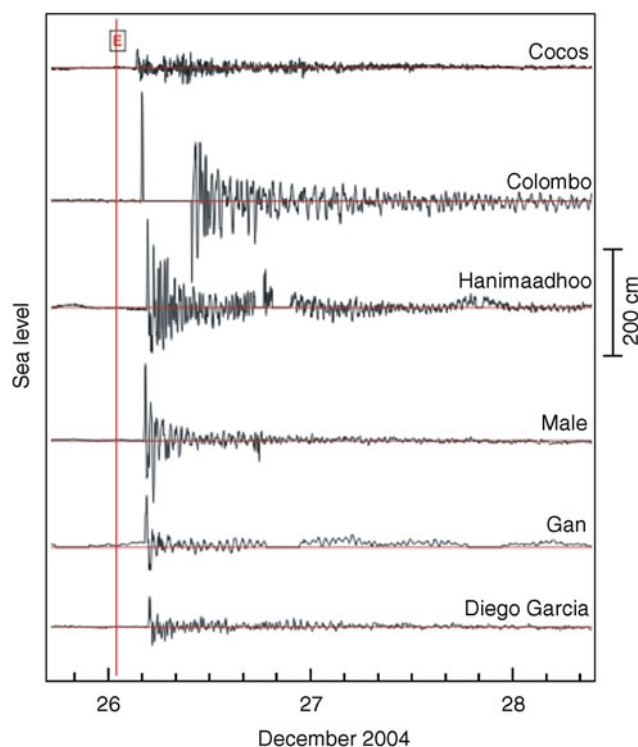
At a finer spatial resolution, a network of oceanic reefs or individual reef platforms produces a number of distinct transformations in tsunami wave characteristics that are

dependent on the planform configuration, density, and size of the reefs. Where there are extensive linear fringing or barrier reef systems that either adjoin or are close to continental coastlines or high islands, wave energy is dissipated first onto the reefs, then onto the coastline. It is in these reef settings that energy interaction with reefs is most intense and where there is the greatest potential for impacts on reef ecology and geomorphology. These interactions are discussed in more detail later.

In mid-ocean archipelagos and open networks of reef systems, the reef network acts as a semi-permeable membrane to the propagation of tsunami wave energy. Gaps between reefs induce localized refraction and diffraction patterns. The interaction of tsunami with the seabed and reef structures extracts energy from the tsunami.

Where individual roughly circular islands have dimensions comparable to the tsunami's wave length, the wave may refract completely around the island, resulting in amplified wave and run-up height on its leeward side. Such behavior was observed at Babi Island, a conical shaped island approximately 2 km in diameter, as a consequence of the 12 December 1992 earthquake-generated tsunami at Flores Island, Indonesia (Yeh et al., 1993; Minoura et al., 1997). Numerical models and laboratory experiments showed that tsunami waves would have penetrated sheltered areas of Babi with minimum loss of energy (Yeh et al., 1994). Maximum run-up height and velocity were amplified 1.7 and 3.0 times, respectively, on the leeward sides of the island, destroying two coastal villages.





**Tsunami, Figure 2** Tide gauge records of the December 2004 Sumatra tsunami in the eastern and central Indian Ocean (From Fisheries and Oceans Canada, 2005).

### Tsunami shoaling and energy dissipation on coral reefs

The type of wave shoaling varies among reefs of different structures and geographic locations. Such differences can have significant implications for the way energy is released on, or adjacent to, coral reefs and the subsequent ecological and geomorphic impacts.

Mid-ocean atolls are characterized by small dimensions, large surrounding ocean depths (in excess of 3,000 m), and very steep underwater structures (slopes reaching 40°). Consequently, atoll islands present a steep and small obstacle to tsunami propagation and present limited potential for shoaling and result in less impact (Searle, 2006; Obura and Abdulla, 2005). For example, during the Sumatran tsunami, wave heights in Maldives atolls were raised from mid-ocean heights of 0.7 m to heights of only ~2.5 m (Titov et al., 2005; Figure 2). In these circumstances the wave structure remains stable (does not break) and the wave can propagate across coral reefs and over associated reef landforms (islands and coastal plains), inundating coastal areas in the form of a progressively rising swell over distances of up to 10 km in the near field (Okal, 2009).

In contrast, where fringing and barrier reefs are located on broad and low gradient continental shelves (<10°) tsunami can shoal rapidly and break as they interact with

coral reefs and coastlines. In such instances, the waves hit the shoreline as a turbulent bore (broken wall of water) with strong flow (Heller et al., 2005). Such waves lose their energy through turbulent friction and dissipation with the sea floor, reef structure, and land surface. However, due to the high velocity of tsunami waves, turbulent bores can flow several kilometers across the land surface (Jaffe et al., 2006). These turbulent bores can be destructive to seafloor, reefs, and shoreline, and the dissipation of energy at that stage influences, to some degree, the extent and force of inland propagation of the wave.

Some authors note that coral reefs can act as effective buffers to shoreline impacts of tsunami (e.g., Kunkel et al., 2006; Cochard et al., 2008). Others (Campbell et al., 2007; Paris et al., 2009) note they are not necessarily effective at all. Positioned directly at the interface between shallow marine and terrestrial environments, coral reefs can be one of the first ecosystems to feel the effect of tsunami waves. This role in buffering the influence of tsunami has been proposed by a number of authors (Okal, 2009; Chochard et al., 2008). The surface roughness and shallow depth of reefs and reef flats is able to extract energy from waves close to the coast. Observations supporting this buffering effect have been documented in the Indian Ocean, where Mauritius (which has an encircling reef) experienced significantly less damage than Réunion Island (where the coral reef is absent from much of the shoreline; Okal, 2009). However, other studies (e.g., Campbell et al., 2007; Cochard et al., 2008) suggest that regional comparisons do not support such assertions and tsunami impacts are more locally variable.

Conspicuous aspects of the final interaction of tsunami with coral reefs and reef-associated landforms are the run-up and backwash phases of each individual wave. Run-up heights (the vertical reach of tsunami waves on land) range up to 100 m for the largest paleo-tsunami (NGDC, 2009). In general, the amount of energy tsunami can expend on a reef, adjacent landforms, and human-built infrastructure increases exponentially with increasing tsunami run-up height, and tsunami with run-up depths greater than 10 m cause the most destruction (Okal, 2009). The most vulnerable reef-adjacent landforms are valleys, where subaerial topography contains the wave and elevates the run-up volume. This is most common on reef-fringed continental coastlines or high islands. Numerous studies have highlighted significant local variability in the extent of run-up levels. Indeed the run-up amplitude at any given coast is a complex function of the incident wave characteristics, bathymetry, and coastal topography (Choi et al., 2006; Chavanich et al., 2008; Cochard et al., 2008; Okal, 2009). Plafker's law presents a simple rule of thumb and predicts that maximum run-up does not exceed twice the amplitude of the seismic movement on the fault (Okal and Synolakis, 2004).

The backwash phase is characterized by extreme seaward directed flow, as the unbroken wave is reflected off the land surface or as broken bores drain seaward. However, unlike the run-up phase which is generally perpendicular to the coastline, backwash flow patterns are controlled by

topography, with extreme flows occurring oblique to the shoreline as flow is directed into existing channels (Gelfenbaum and Jaffe, 2003; Umitsu et al., 2007; Paris et al., 2009). These seaward-directed flows are able to preferentially scour coastal landforms but also deliver vast quantities of terrestrial sediment and debris (e.g., trees, building materials) to the coastal margin that promote direct physical impacts on coral reefs (Umitsu et al., 2007; Worachananant et al., 2007; Paris et al., 2009).

In low-lying reef islands, waves can propagate directly across island surfaces as unbroken wave forms as described by Kench et al. (2007, 2008) in the Maldives. Due to the lack of relief in these reef island settings there may be no backwash phase of the wave. Rather, island flood water is ponded on the island surface (Kench et al., 2007). In these circumstances, backwash is not a significant factor in driving change in the geomorphic or ecological structure of coral reefs.

### Impacts of tsunami on coral reef ecology

Paleo-tsunami studies based on interpretation of sediment deposits suggest that mega-tsunami may have catastrophic impacts on reef communities, physically destabilizing and excavating reef coral and framework (Scheffers et al., 2009). However, until the Sumatran tsunami in 2004 very little observational research had been undertaken on the effects of tsunami on the ecology of coral reefs (Brown, 2005; Hagan et al., 2007). A number of studies undertaken immediately following the 2004 event have provided new insights into the types of ecological damage encountered as a consequence of large tsunami events.

Assessments of reef ecological condition following the Sumatran event collectively indicate that tsunami had a relatively minor impact on reef condition and ecological composition when compared with documented impacts of cyclones, bleaching episodes, and anthropogenically-forced change in reef systems (Baird et al., 2005; Brown, 2005; Gunn et al., 2005; Campbell et al., 2007). A number of studies were able to revisit reef monitoring sites that had been established prior to the tsunami, to document specific changes in reef ecological condition. For example, Phongsuwan and Brown (2007) present data from 18 fringing reef sites on the west coast of Thailand and show that at over 60% of sites there was little or no damage to reef ecological condition (Figure 3a). At only 13% of sites were reef communities severely damaged. While gross impacts were considered minor there was ample evidence of dramatic changes in the physical and ecological condition of reefs at the local scale. The range of impacts is described below based primarily on observations from the Sumatran tsunami.

### Earthquake-related impacts

While not a direct impact of tsunami waves, the precursor earthquake of the Sumatran tsunami promoted differential uplift and subsidence of fringing reef systems. It is estimated that 1,000 km of coral reef, along the plate boundary from the Andaman and Nicobar islands to Sumatra, have

been tectonically affected (Bilham, 2005). One of the most dramatic effects on reef systems was uplift of some fringing reefs by 1.6 to 2.0 m on the west coast of the Andaman Islands (Sieh, 2005; Searle, 2006; Liew, 2008). Uplift had a number of impacts on reef communities. First, uplift caused extensive mortality of uplifted corals due to subaerial exposure of reef flat communities (Hagan et al., 2007; Figure 3b). For example, Sieh (2005) reported microatolls were raised by 1.5 m on the northwest coast of Simeulue Island, Aceh Province. Second, uplift raised subtidal reef front coral into the intertidal reef flat zone, which may have medium-term consequences for coral adaptation and survival (Hagan et al., 2007). Associated with uplift, Bahuguna et al. (2008) report the development of cracks in the reef structure. Collectively, such fissures are likely to reduce the structural integrity of the reef system.

In contrast, other tracts of reef underwent subsidence by up to 2.5–3.0 m (Searle, 2006; Hagan et al., 2007), which has displaced shallow water communities to deeper reef zones. While this subsidence has created new accommodation space for coral growth on reef tops (see *Accommodation Space*), there have also been subtle changes in hydrodynamics and water temperatures that may affect species' survival and reef community structure in the medium-term (see *Corals: Environmental Controls on Growth*).

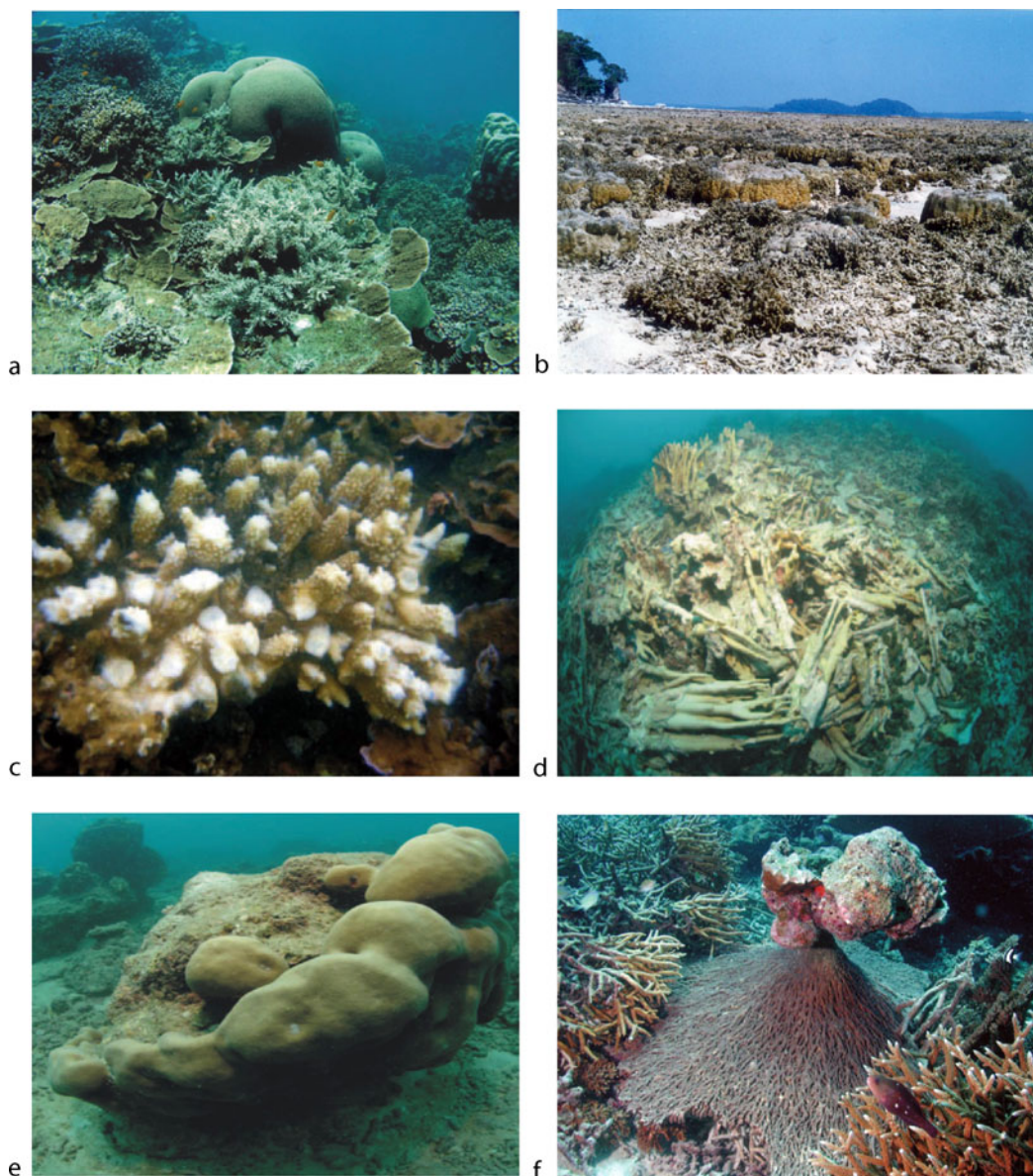
### Tsunami impacts on corals and reefs

Tsunami impact can be differentiated into a number of categories. Mechanical damage to corals following the Sumatran tsunami was observed on many reefs. This included the breaking of coral branches, collapsing of branching colonies and the fracture of massive coral (Baird et al., 2005; Worachananant et al., 2007; Figure 3c and d). This physical breakage of corals is attributed to impacts by water-borne debris during the uprush and backwash phases of tsunami flow. Such debris might include marine and/or terrestrial debris (e.g., trees).

The overturning of individual coral colonies was prevalent in most studies (Figure 3e and f). However, the depth range and types of corals susceptible to overturning varied between studies. For example, Baird et al. (2005) and Campbell et al. (2007) reported that overturning was most common for massive corals at depths greater than 2 m, and which were attached to unconsolidated substrates (Figure 3e). This is consistent with the observation that it is the mechanical strength of attachment of corals to substrate which is of overriding importance in coral stability as opposed to the integrity of the coral growth form (Massel and Done, 1993; Madin, 2005; Madin and Connolly, 2006). Studies from the reefs of Thailand indicated that overturned, massive, and tabulate coral colonies were limited to shallow water sections of reefs (Brown, 2005; Phongsuwan and Brown, 2007; Chavanich et al., 2008; Figure 3f).

Transport of large coral colonies is an additional physical change in coral colonies. Baird et al. (2005) report movements of large massive colonies from the reef front (water





**Tsunami, Figure 3** Types of ecological damage observed on coral reefs following the Sumatran tsunami (26 December 2004). (a) Unaffected mixed coral community on upper reef slope, Surin Islands (From Phongsuwan and Brown, 2007). (b) Uplifted coral reef, Andaman Sea (From unknown). (c) Broken branches in an *Acropora* sp. in 0.5 m water depth (From Campbell et al., 2007). (d) Shattered blue coral *Heliopora coerulea* at 3 m water depth Telok Beluhan, Pulau Weh (From Hagan et al., 2007). (e) Overturned *Porites* sp colony at 4 m water depth, north coast Aceh Province (From Hagan et al., 2007). (f) Overturned table coral at 3 m water depth, Ari atoll, Maldives (From Gischler and Kikinger, 2007).

depths >10 m) to reef flat surfaces (Figure 4a and b). Goto et al. (2007) identified more than 1,000 1 m size coral blocks transported from the reef front to reef flat surface at Pakarang Cape, Thailand.

Sedimentation on reefs is an additional impact reported in most studies. Sedimentation is manifest in a number of ways. First, through deposition of remobilized deeper marine sediments smothering corals as tsunami waves propagated across the reef (Baird et al., 2005; Chavanich, et al.,

2007; Kelletat et al., 2007; Worachananant et al., 2007; Gischler and Kikinger, 2007; Bahuguna et al., 2008; Figure 4c and d) and deposition of terrestrial-derived sediments as a consequence of backwash flow. Deposition can smother living corals and promote coral mortality. Furthermore, at some sites transport of coarser sand and gravel sized sediments buried, or partially buried, corals leading to coral mortality (Campbell et al., 2007; Worachananant et al., 2007; Kench et al., 2008; Figure 4e and f).





**Tsunami, Figure 4** Examples of sediment movement and impacts on coral reefs following the Sumatran tsunami (26 December 2004). (a) Large *Porites* colony, 3 m diameter, transported from the reef and buried in the beach at Pulau Beras, Aceh (From Campbell et al., 2007). (b) *Porites* boulder situated 50 m from beach at Pulau Beras (From Baird et al., 2005). (c) Healthy colony of *Acropora muricata* in 1 m water depth, Aceh, November 2000 (From Campbell et al., 2007). (d) The same colony as in Figure 3c in April 2005. The coral tissue has been smothered by sediment stirred up by the tsunami (From Campbell et al., 2007). (e) *Porites* colony 1.5 m diameter, half buried in coarse sand and gravel at 4 m water depth, Aceh (From Baird et al., 2005). (f) Reef flat corals buried by sand as a result of beach extension across reef flat at Hulhudhoo Island, Baa atoll, Maldives (From author).

Campbell et al. (2007) and Kelletat et al. (2007) also suggest that the sediment transport regime of some reefs has altered as a consequence of delivery of increased sediment volumes to reefs. The constant remobilization of finer material and their smothering effect have caused delayed and localized mortality of corals.

The reported range of ecological impacts resulting from the Sumatran tsunami shows marked differences from the ecological impacts associated with cyclones

(Baird et al., 2005). While cyclone damage is also patchy (Woodley et al., 1981; Done, 1992b; see *Tropical Cyclone/Hurricane*), it is unusual for shallow sections of tsunami-impacted reefs to avoid damage, and fragile colonies (branching and tabular) are generally disproportionately affected compared to massive colonies. Such differences have been attributed to differences in wave energetics as they interact with reefs. Cyclonic waves impact upon reefs repeatedly over periods of several hours. While the

waves may be large, they carry and release their energy at upper layers of the water column and, therefore, impact shallow water reef zones: deeper parts of the reef are often indirectly affected by avalanches (Baird et al., 2005). In tsunami, by contrast, there are generally only a small number of waves generated on any given event. These waves transfer energy throughout the water column so that hydrodynamic stress is transferred directly to greater depths (Yeh et al., 1994), they can remobilize deeper sediments, and they can damage deep slope coral communities. Furthermore, a characteristic feature of tsunami is marked draw-down of water level prior to tsunami impact. Entire subaerial exposure of reef flat surfaces occurred during the Sumatran event. Consequently, as tsunami waves reinvaded the reef, they interacted directly with the reef-top sediments, structure, and coral communities (Kench et al., 2008; Paris et al., 2009).

### Patterns of impact

While individual studies have attempted to interpret the underlying factors that expose reefs to tsunami impacts at the site-specific scale, comparative analysis between studies (at the regional to global scale) suggests simple explanations are not possible. For instance, some studies of the Sumatran tsunami (e.g., Cochard et al., 2008) attributed the apparent localized variability in impact severity to the state of reef health (e.g., Cochard et al., 2008). However, this was not corroborated by studies of many near-field sites in the Andaman Sea, which suggest a threshold of wave energy above which reef condition has little effect on tsunami impacts (Paris et al., 2009). Overturning and transport of massive colonies occurred both at depth in the Acehese reefs (Baird et al., 2005; Campbell et al., 2007) and on shallow reef sites (coast of Thailand; Chavanich et al., 2008). A number of studies report higher rates of damage in reef passages, where currents were forced to accelerate during tsunami wave flow (Goffredo et al., 2007; Worachananant et al., 2007). Foster et al. (2006) showed the highest frequency of overturned corals occurred on fringing reefs inside bays as opposed to headland reefs.

A synthesis of post-tsunami surveys indicates a number of preconditioning factors that make reefs susceptible to damage. These factors include: relative exposure of reefs to wave impact; reef slope and nearshore bathymetry that control wave shoaling and breaking potential; the water depth across the reef surface; the ecological composition of reef communities, and; the substrate type upon which corals are attached. Due to this combination of factors, damage to reef communities is highly variable and difficult to predict (Baird et al., 2005; Campbell et al., 2007; Chavanich et al., 2008).

At issue, in evaluating the long-term consequences of tsunami on reef ecology is whether impacts will persist on reefs. Whereas reef losses to uplift are irreversible, the localized, patchy, and minimal level of the Sumatran tsunami impacts on corals suggests that the reefs there will recover over a 5–10-year period (Baird et al., 2005;

Brown, 2005; Hagan et al., 2007). Such optimistic scenarios are based on the presence of unaffected sections of reef to act as sources of larvae for coral regeneration.

### Geomorphic impacts on reefs and reef associated landforms

Despite the extreme size and speed of larger tsunami and the devastating impacts such events have on coastal communities and infrastructure, few studies have evaluated the geomorphic implications of tsunami. The majority of studies of geological impacts of tsunami have focused on the interpretation of sediment deposits to discriminate the presence, magnitude, and frequency of extreme wave events and their flow characteristics. However, definitively attributing such deposits to tsunami has proved problematic in reef environments because cyclonic wave events produce similar sedimentary units (e.g., Bourrouilh-Le and Talandier, 1985; Nott, 1997). Consequently, the differentiation of paleo-tsunami from other extreme wave event deposits has been the subject of considerable discussion (see Hearty, 1997; Nott, 1997, 2003; Goff et al., 2004; Noormets et al., 2004; Morton et al., 2008; Scheffers et al., 2009).

Tsunami events over the past 20 years, however, have provided modern analogues to improve our understanding of the types of geomorphic change and sedimentary deposits they produce. For example, observations of the erosional and depositional signatures associated with the 1992 event at Flores, Indonesia is one of the earliest attempts to directly examine detailed geomorphic effects of tsunami in a reefal environment (Yeh et al., 1993). Subsequently, a number of studies have examined the sedimentary deposits formed by recent tsunami at Mindanao, Philippines in 1992 (Besana et al., 2004), Rajegwesi, Java, Indonesia in 1994 (Dawson et al., 1996), Papua New Guinea in 1998 (Gelfenbaum and Jaffe, 2003), and most notably the Sumatran mega-tsunami in 2004, on which there have been numerous reports from around the Indian Ocean.

Collectively, these paleo-studies and modern analogues identify a range of geomorphic impacts. These impacts can be divided into those affecting reef structure and those influencing associated reef sedimentary landforms (reef islands and coastal plains adjacent to fringing and barrier reefs). The geomorphic changes in each component of the reef system are mediated by the mobilization, transfer, and deposition of reefal sediment.

### Geomorphic impacts on coral reefs

Uplift or subsidence of coral reefs, as a consequence of earthquakes that trigger tsunami, are major and immediate changes in the gross structure of coral reefs with respect to sea level (discussed above). Based on large volumes of reef-derived material deposited on land, paleo-tsunami studies suggest that mega-tsunami can impact on the living veneer and structure of reefs, decimating living coral communities, and degrading or removing the geomorphic structure of a coral reef. For instance, coral reefs were present on the windward coast of Bonaire and Curaçao in the

Pleistocene and early-mid Holocene, but are currently absent (Pandolfi and Jackson, 2001), manifest instead as approximately 4 million tons of the Holocene remains (coral fragments and boulders) on the adjacent coastal plain (Scheffers et al., 2009). Consequently, the frequency and intensity of large tsunami and other extreme wave events may determine whether reefs can persist, develop, or perish in a particular location (Blanchon et al., 1997; Morton et al., 2008).

While changes in reef structure and elevation may occur at the event timescale (hours), the resulting alteration of the process regime may be of medium to long-term duration (years to centuries). Reef elevation with respect to sea level is a critical control on the ability of reefs to dissipate background ocean wave energy (Roberts et al., 1977; Symonds et al., 1995). As water depth increases at the reef edge, the period of time that incident wave energy can propagate across reefs also increases (Kench and Brander, 2006). It is this energy that is available to entrain and transport sediment on reef surfaces promoting erosion or reconfiguration of island shorelines (Kench et al., 2009). Consequently, geomorphic processes can be expected to close down across reefs as a consequence of uplift in a similar fashion to the closing of the mid-Holocene high energy window (Hopley, 1984). In contrast, geomorphic processes are likely to be reactivated following subsidence or loss of reef structure as water depth over reefs increases, as modeled by Sheppard et al. (2005) (see *Accommodation Space; Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity*).

### Geomorphic impacts on reef-associated sedimentary landforms

Tsunami can promote a range of geomorphic responses in sedimentary shorelines deposited on or adjacent to coral reefs. Such geomorphic changes are mediated by the redistribution of reefal sediment within the reef system.

Shoreline erosion (net loss of land) is a commonly cited effect of tsunami wave interaction with sedimentary landforms. For instance, extensive erosion of low-lying coastal plains was reported on the coast of Banda Aceh, following the Sumatran tsunami of 2004 (Paris et al., 2009). Apart from places where erosion was arrested by the presence of beachrock, there was a substantial horizontal retreat of the shoreline and destruction of sand barriers protecting lagoons, producing a step-like displacement of the active shoreline. Along a 9.2 km stretch of shoreline at Lhok Nga Bay, the mean rate of shoreline displacement was approximately 60 m and involved reworking of 276,000 m<sup>3</sup> of sediment (Paris et al., 2009). Coastal erosion was also identified at other reef locations throughout the Indian Ocean, although magnitudes of erosion were much less than those at Lhok Nga Bay (e.g., Richmond et al., 2006). Based on a comparison of pre- and post-tsunami surveys of reef island morphology, Kench et al. (2006) found that erosion of the vegetated core of islands in the Maldives ranged from

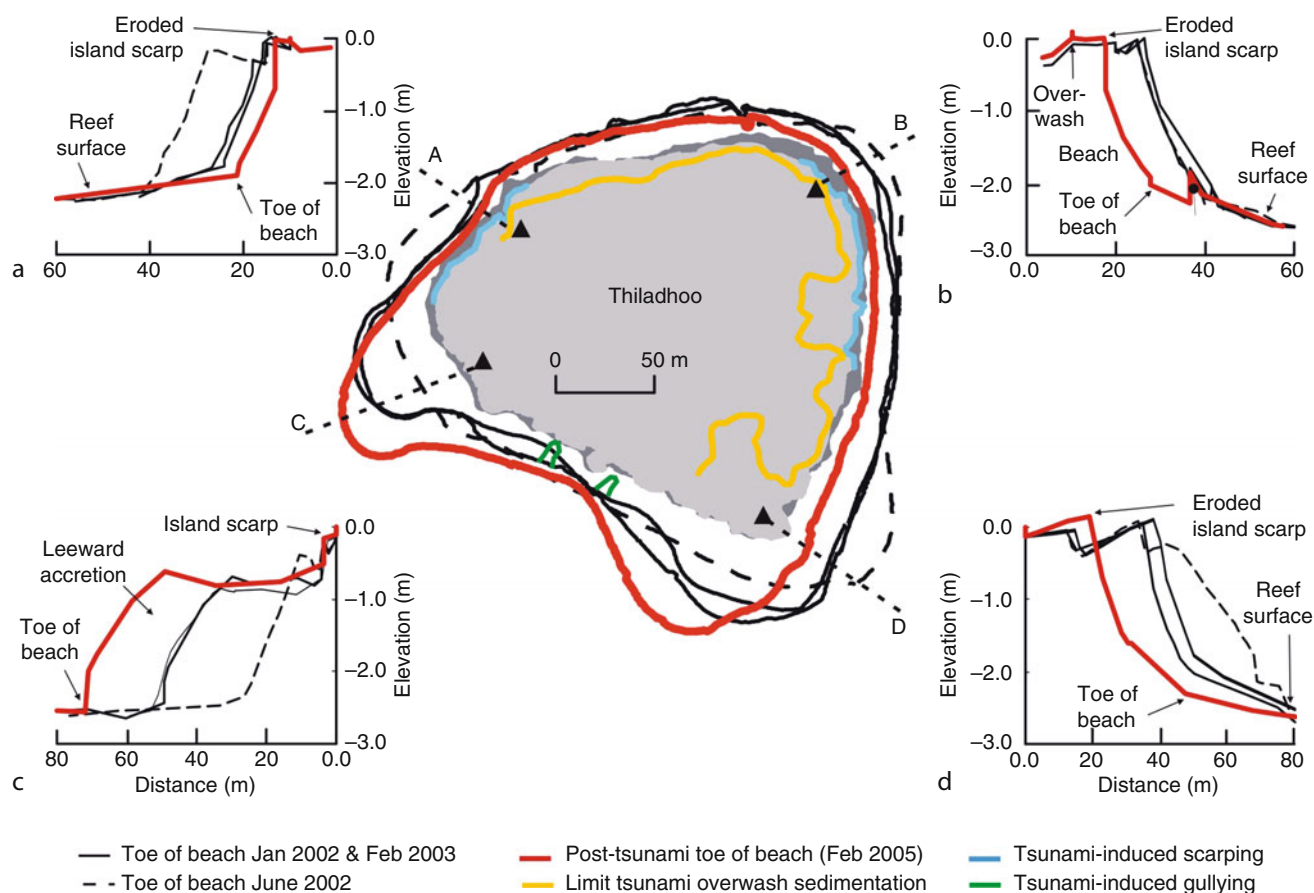
1–9% of island area (Figure 5). Physical evidence for coastal erosion includes stripping of beaches, development of erosional scarps in the vegetated core of islands, scour and collapse of vegetation at island shorelines, erosional trenches on the lagoon sides of islands, and erosional contacts in terrestrial soil horizons (Figure 6).

Proximity (exposure) to tsunami source is a factor determining the magnitude of coastal erosion. However, like ecological impacts, the magnitude of reported erosion is spatially variable. Other factors influencing the extent of erosion include elevation of the seaward margin of the coast, differences in the way tsunami interacted with the shoreline, the volume of sediment present at shorelines to act as a buffer to tsunami impact, and the presence or absence of vegetation. On fringing reef coasts backed by steep terrain, the shoreline experiences both uprush and backwash flow. Consequently, the coastal deposits experience a combination of landward and seaward-oriented turbulence and sediment transport (Paris et al., 2007, 2009). By contrast, on atoll islands in the Maldives, there was no backwash. Due to the low-elevation of these atoll islands (<2 m above mean sea level), the tsunami waves were able to wash over the outer ridge, the lack of relief precluding backwash. Rather, the basin morphology of island surfaces allowed water to pond for up to 6 weeks after the tsunami (Kench et al., 2007, 2008). Water ponding promoted salinization of the groundwater tables and salt burn of island vegetation. On some islands, this water flowed through the island sands and surfaced on beaches producing gully erosion of the upper beach and vegetated shoreline. In some southern atolls of the Maldives, there was complete overwash of the islands. This overwash produced minimal geomorphic impacts on islands, but it did cause erosional shore-parallel trenches (up to 2 m deep and 5–10 m wide) on the lagoon shorelines of islands (Gunn et al., 2005; Richmond et al., 2006; Figure 6d). These features are thought to result from wave turbulence, which was unable to erode island surfaces due to the dense vegetative cover, but was able to scour loose unconsolidated sediment along the lagoon shoreline.

The volume of sediment stored at the shoreline prior to tsunami impact also plays a significant role in the degree of shoreline erosion. On Maldivian reef islands, where plentiful volumes of sediment were stored in the beaches, this material was able to absorb impact of the tsunami and shoreline erosion was minimal (Kench et al., 2008). By contrast, locations with little or no beach had greater erosion.

Perhaps the most striking geomorphic outcome of tsunami is the creation and aggradation of coastal landforms: the landward deposition of reefal material. The origins and depositional history of these units can be determined using their sedimentary characteristics, extent, and morphology. Landward deposition of sand sheets has been observed on numerous reef-fringed shorelines and low-lying atoll islands, where sediment rich coasts have undergone net erosion (Figures 5 and 7a–d). Typically, sand sheets take the form of landward tapering wedges of sand, which exhibit bedding that results from multiple wave flow



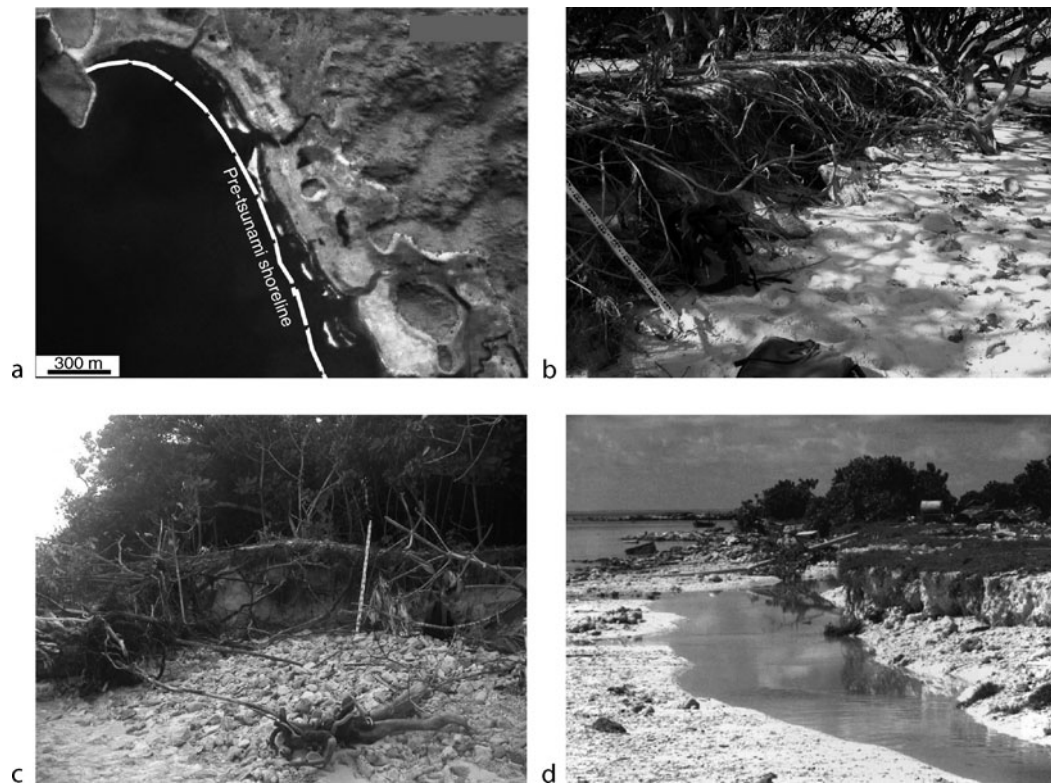


**Tsunami, Figure 5** Summary of geomorphic impacts of the December 2004 Sumatra tsunami on Thiladhoo Island, South Maalhosmadulu atoll, Maldives. Thiladhoo Island in center showing pre- and post-tsunami vegetated shoreline and toe of beach positions. Light gray denotes vegetated island core. Note: erosion of vegetated shoreline along the northwest, northeast shorelines (dark gray); landward movement of toe of beach position on exposed northeast shoreline; extension of depositional zones on the western and southern lobes beyond the surveys previously undertaken at the same stage of the northeast monsoon (January 2002, February 2003); shift in beach position resulting from the southwest monsoon conditions (*dashed line*); and Limit of landward extension of overwash sand sheet deposition (*yellow line*). (a–d) Island to reef topographic surveys showing landward movement of the vegetated scarp (a, b, c) and significant deposition on western lobe smothering live coral on the reef flat (d) (From Kench et al., 2006).

across the land surface (Figure 7c). The landward extent of these sand sheets appears correlated with the magnitude of tsunami, coastal topography, and sediment supply. For example, on Babi Island sand sheets ranging in thickness from 0.05 to 0.1 m extended up to 500 m landward as a consequence of the Flores tsunami in 1992 (Minoura et al., 1997). At Lhok Nga Bay, Banda Aceh, sand sheets were identified up to 3.5 km landward and ranged up to 0.8 m thick following the Sumatran tsunami (Figure 7d). In the Maldives, the same event produced continuous and discontinuous sand sheets up to 0.3 m thick and extending up to 60 m landward on the outer rim of atoll islands (Kench et al., 2006, 2008; Figures 5 and 7). Few examples of such sand sheets have been identified in paleo records suggesting these sedimentary units do not retain their integrity over geological timescales (Kench et al., 2006). However, these deposits are

geomorphically important as they contribute significant quantities of sediment to coastal landforms ( $10^2$ – $10^6$  m<sup>3</sup>) and represent net addition to the land surface. In the context of low-lying reef islands and coastal plains these deposits represent vertical aggradation of the land surface that can become vegetated and occupied by humans. Over geological timescales, the frequency of tsunami may be important in vertical building of reef-associated landforms.

Landward deposited ridges and ramparts comprising a mix of large coral boulders, gravels, and sand-size materials derived from adjacent coral reefs have been attributed to tsunami in a number of studies (e.g., Scheffers et al., 2009; Figure 7e and f). These geomorphic features can be up to 4 m in elevation and 30–400 m in width, thus representing significant additions of material to coastal sediment units ( $\sim 10^6$  m<sup>3</sup>; Morton et al., 2008;

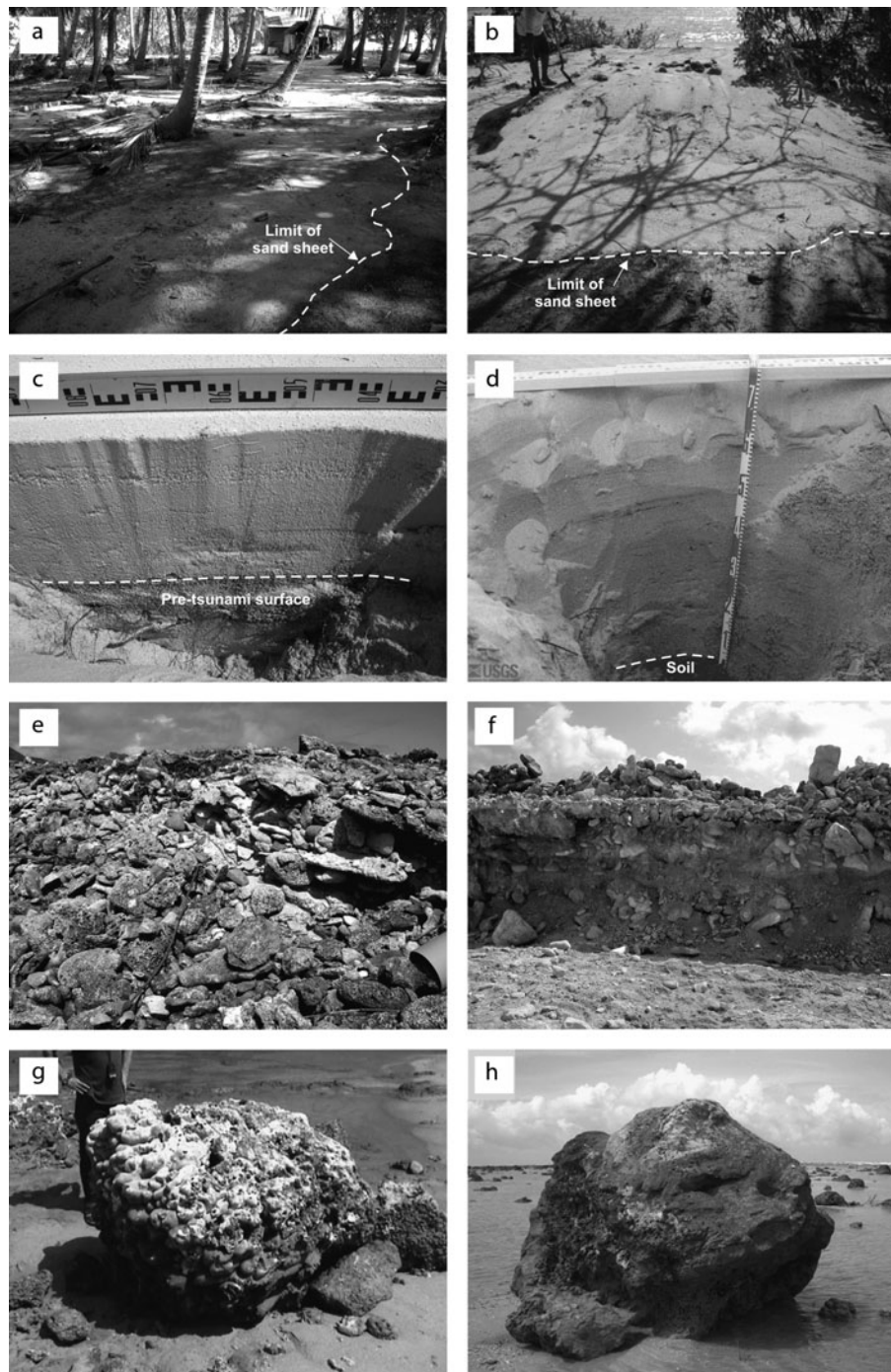


**Tsunami, Figure 6** Examples of shoreline erosion resulting from the December 2004 Sumatra tsunami. (a) Satellite image showing large-scale coastal retreat in the north part of Leupung Bay, Sumatra (From Paris et al., 2009). (b) Lateral scour of reef island shoreline exposing root systems in South Maalhosmadulu atoll, Maldives (From author). Scarping of reef island shoreline in South Maalhosmadulu atoll, Maldives (From author). Scarping and trench scour on lagoon shoreline of Vilufushi Island, Thaa atoll, Maldives (From Richmond et al., 2006).

Scheffers et al., 2009). In the example of Bonaire and Curaçao (described earlier), landward delivery of the detrital Holocene reef matrix has formed a sequence of ridges and ramparts that extend across several kilometers of the coastal margin. Consequently, individual tsunami rapidly deposit large volumes of reefal material, and the frequency and timing of events determine the long-term development of the morphology of coastal plains. However, considerable debate exists as to whether such deposits are attributable to tsunami or to cyclone waves. Morton et al. (2008) argue, there are no known examples of historical tsunami depositing a laterally extensive, high ridge of coarse clasts in the Caribbean Islands. Furthermore, no such deposits were reported following the Sumatran mega-tsunami. However, Scheffers et al. (2009) propose key discriminatory features such as clast abrasion, internal sedimentary structure, ridge orientation, and width can be used to determine the relative role of the two phenomena in deposit formation.

Boulder fields are perhaps the most commonly cited product of the landward transfer of nearshore material under tsunami flow. In reef settings, paleo studies have identified boulders (reef framework and coral bommies) up to

8 m diameter and weighing more than 260 t (Scheffers et al., 2009). While they represent the addition of very large individual reef blocks to the land surface (Figure 7g and h), they can be quantitatively less important than other depositional forms. Such deposits have attracted great scientific interest as diagnostic indicators of extreme wave events (Morton et al., 2008). Of note, Goto et al. (2007) examined boulder deposits on the west coast of Thailand and found that more than 1,000 coral boulders were transported from the reef front to the reef flat, although none were deposited on land (Figure 7h). A number of studies have highlighted a significant disparity between the physical evidence of geomorphic change observed from the Sumatran mega-tsunami and interpreted paleo mega-tsunami deposits. In particular, paleo-tsunami studies have identified more spectacular boulders (megablocks), more extensive boulder fields, and extensive coarse clast ridges (Scheffers and Kelletat, 2003; Robinson et al., 2006; Kelletat et al., 2007; Morton et al., 2008; Scheffers et al., 2009). Such differences have caused some researchers to question whether the Sumatran event provides a good analogue for the impacts that can be expected from mega-tsunami. Paris et al. (2009) suggest that the geomorphic impact of this event is



**Tsunami, Figure 7** Examples of types of tsunami sedimentation and geomorphic products. (a) Landward limit (60 m) of continuous overwash sand sheet, Dhakandhoo Island, Maldives (From author). (b) Small sand sheet extending across reef island margin, South Maalhosmadulu atoll, Maldives (From author). (c) 0.3 m thick tsunami sand sheet on outer margin of Thiladhoo Island, Maldives (From author). (d) 0.75 m thick sand sheet overlying dark soil horizon (base of trench) at Lampuuk, northwest Sumatra (From Richmond et al., 2006). (e) Seaward front of inferred tsunami ridge along the southern coast of Anguilla (dated at 1,500 years before present; From Scheffers et al., 2009). (f) Inferred coarse clast tsunami deposit, Caribbean. Note chaotic and bimodal texture of internal structure (From Scheffers et al., 2009). (g) Ten tons coral boulder at Nai Harn Noi Beach, Thailand deposited by the Sumatra tsunami (From Kelletat et al., 2007). (h) Large 2 m diameter boulder (one of more than 1,000) deposited at Pakarang Cape, Thailand (From Goto et al., 2007).



more impressive in its spatial extent (influencing many countries around the Indian Ocean basin) rather than its intensity. It has been suggested that the slow impulse movement (7 min) along the fracture zone that generated the tsunami produced a wave train that was less intense than major paleo-tsunami (Kelletat et al., 2007).

## Summary

Tsunami are extreme wave events that can be devastating to coastal communities. These events, while infrequent on human timescales, are relatively common at geological timescales and have impacted on global reef systems throughout the history of their geomorphic development. The impact of tsunami on coral reef systems has largely been interpreted from paleo-tsunami reconstructions and in more recent years studies of modern tsunami impacts. In this regard, the Sumatran mega-tsunami has provided a rich source of analogues. Collectively, these studies have identified a wide range of ecological and geomorphic impacts on reef systems ranging from paleo interpretations of total reef destruction and transfer of debris to build coastal landforms to minimal ecological and geomorphic impacts. Indeed, the tragic Sumatran mega-tsunami in 2004 generally had relatively minor ecological and geomorphic impacts on reef systems, despite spectacular localized impacts. Such results signify either misinterpretation of impacts in paleo studies or simply that deposits represent the outcomes of even larger extreme wave events.

Studies highlight extreme spatial variation in magnitude and type of tsunami impact. Underlying factors that predispose reefs and reef landforms to impact include: tsunami wave height; ocean bathymetry, reef morphology and health; coastal topography; sediment volume stored at the shoreline, and; coastal vegetation.

While many of the ecological and geomorphic impacts identified represent immediate responses to extreme wave forces, these changes may also trigger longer-term changes in ecological and physical process regimes that can impact reef systems. Examples include the increased flux of sediment on reef systems that may reduce water quality and impact on reef health; a shift in energetics of reef hydrodynamic processes, and; disruptions in sediment budgets and, therefore, geomorphic equilibrium of reef landforms (Kench et al., 2008).

At geological timescales, coral reefs and reef-associated landforms have been subject to multiple tsunami throughout the history of their geomorphic development. Consequently, the frequency and magnitude of events is likely to not only control reef persistence but influence development of sedimentary landforms. However, few studies have been able to elucidate these dynamics beyond the role of individual events.

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## Cross-references

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## TURBID-ZONE AND TERRIGENOUS SEDIMENT-INFLUENCED REEFS

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## Definition

*Turbid-zone and terrigenous sediment-influenced reefs.* Coral reefs that develop in environments that are either directly, or indirectly, under the influence of terrigenoclastic sediments. Direct influence is exerted in those sites where high levels of terrigenoclastic sediment accumulation or sediment flux occur. Indirect influence is exerted where fine-grained sediments are continuously or episodically in suspension, thus influencing reef development by elevating



turbidity levels. Typically, the reefs developing under these conditions are more restricted both spatially and bathymetrically than their clear-water counterparts, but can still harbor thriving and relatively diverse coral communities and exhibit high coral cover. Such reefs also represent important localized sites of carbonate production within otherwise terrigenous sediment-dominated marine environments.

## Introduction

High levels of terrigenous sediment input and elevated turbidity regimes have been widely identified as a major limiting factor for coral reef development (Buddemeier and Hopley, 1988). These limitations have been linked not only with the ongoing supply of terrigenoclastic sediments from adjacent mainland (fluvial) sources, but also with past phases of terrigenous sediment accumulation (especially reworking of relict lowstand fluvial sands and gravels, and soils) and with ongoing sediment flux within the marine environment. The various sources or pathways of terrigenoclastic sediment input and influence vary in significance within different marine settings and act to influence reef development in different ways over a range of temporal and spatial scales. In some environments, major changes to catchment sediment yields, often linked to changing land-use practices, can exert a major influence on coral community structure and reef zonation, especially where the modified marine environmental conditions far exceed the background conditions under which the existing reef communities evolved (e.g., Cortés and Risk, 1985). Under such conditions, studies predict identifiable shifts in coral cover, diversity and growth rates, and change in coral fecundity (reviewed in Fabricius, 2005). Often, the timescales and longevity of any such changes are complex to predict and may depend upon the adaptability of the coral community. In this context, several studies have documented the resistance mechanisms utilized by corals to cope with “high” sedimentation rates (reviewed in Sanders and Baron-Szabo, 2005), while other studies have documented shifting feeding regimes (changes from predominantly phototrophic to heterotrophic feeding strategies) under higher turbidity conditions (Anthony, 2000, 2006).

However, where the timescales of terrigenous sediment input/accumulation are rather longer, and where coral communities have developed that are more adapted to deal with the ongoing/episodic stresses imposed by high-sediment input/flux regimes, ecological impacts may be less apparent (e.g., Perry et al., 2008). Indeed, the long-term (millennial timescale) persistence of coral reefs within modern marine environments that are under direct terrigenoclastic sediment influence, combined with the numerous descriptions of mixed carbonate (reefal):terrigenoclastic facies in the rock record, provides clear evidence not only of the potential for corals to settle and colonize sedimentary substrates under these conditions, but also for sufficient rates of carbonate framework and sediment production to allow both vertical reef growth and lateral reef accretion.

The reefs that form in these environments represent important localized sites of carbonate production and

biodiversity within areas otherwise dominated by terrigenoclastic sediment accumulation. They form within a wide range of coastal and shallow marine settings (e.g., along open sedimentary coastlines, within muddy coastal embayments, and around high continental islands), have established above a wide range of sedimentary substrates (subtidal sands and muds, deltaic sands, and gravels), and can be delineated from their clear-water counterparts on the basis of their geomorphology and their internal facies/framework fabrics. Available evidence suggests that reef development in these settings may be somewhat opportunistic, with reefs establishing in areas of low net sediment accumulation, but that once established they can grow rapidly to sea level through often narrow vertical accommodation space windows (see Chapter *Accommodation Space*). In some settings, where seafloor substrates permit, such reefs undergo significant seaward progradation, with accretional/progradational histories lasting over millennial timescales despite ongoing terrigenous sediment influence. In other cases, more episodic phases of reef “switch on” and “switch off” may occur as a function of more limited vertical and seaward accommodation space availability and/or nearshore sediment morphodynamics. Given the clear potential for reef building to occur under these conditions, the widespread view that terrestrial sediment inputs inherently suppress or inhibit reef-building potential is probably too simplistic. Rather it is better to consider the reefs that develop in these settings as being one type of a spectrum of reef-building states that are controlled by prevailing marine environmental conditions (see Perry and Larcombe, 2003).

## Terrigenoclastic sediments and turbidity as a limit to coral reef growth

As outlined above, the input and accumulation of terrigenoclastic sediments, and any associated reworking or flux of fine-grained sediment that results in elevated turbidity regimes, can act as a limiting factor to coral growth and reef development. The nature of, and controls upon, these limiting factors and their potential to impact coral survival and reef development are, however, markedly different. Specifically, terrigenous sediment inputs can impact upon coral growth and survival in two main ways: by elevating sedimentation rates and by increasing water turbidity.

## Sedimentation

Sediment accumulation (the downward flux and deposition of sediment on the seabed) can impact upon coral physiology because of the excessive energy requirements made on corals by sediment rejection mechanisms. Under highly elevated rates of sediment accumulation complete burial of corals can occur and, if of sufficiently long duration, this will result in coral death. Where this accumulating sediment is reworked on the seabed the potential for soft tissue abrasion and polyp mortality is high, and this will likely inhibit coral larval settlement. Most typically,

high sedimentation rates are associated with inputs of sediment from proximal fluvial sources, most typically under flood conditions. However, in some environments, terrigenous sediment accumulation primarily represents a legacy of lowstand shelf soils and fluvial sediments that were reworked during the Holocene transgression and transported landward during shelf flooding. In this way, long-term, net terrigenous sediment accumulation can act as an important limiting factor to reef development and a strong control on regional patterns of turbid-zone reef development (discussed below). Threshold sedimentation rates for coral survival are very varied, but widely reported and quoted levels ( $1\text{--}10\text{ mg cm}^{-2}\text{ d}^{-1}$  – slight to moderate impacts;  $10\text{--}50\text{ mg cm}^{-2}\text{ d}^{-1}$  – moderate to severe impacts;  $>50\text{ mg cm}^{-2}\text{ d}^{-1}$  – severe to catastrophic impacts; see Pastorok and Bilyard, 1985) appear to be too low in terms of any short-term (ecological timescale) impacts upon coral growth. These rates can often be exceeded on many inshore coral reefs and would indicate some degree of sedimentation impact even on mid- to outer-shelf reefs (see Hopley and Choat, 1990). A key factor in this context is, however, likely to be the volume, intensity, and duration of any input event, set both against the potential for sediment flux and reworking during and after the event, and against the background sediment accumulation rate. At sites on the inner Great Barrier Reef Shelf, for example, it has been suggested that the resuspension of terrigenous sediment already deposited on the shelf far exceeds that derived from recent fluvial inputs, the latter being relatively insignificant in terms of modifying the sedimentary regime in the region (Larcombe and Woolfe, 1999). An additional, but important, point to make here is that data obtained from sediment traps do not, in many environments, provide a realistic estimate of actual net sedimentation rates because they do not factor in sediment resuspension potential.

### Turbidity

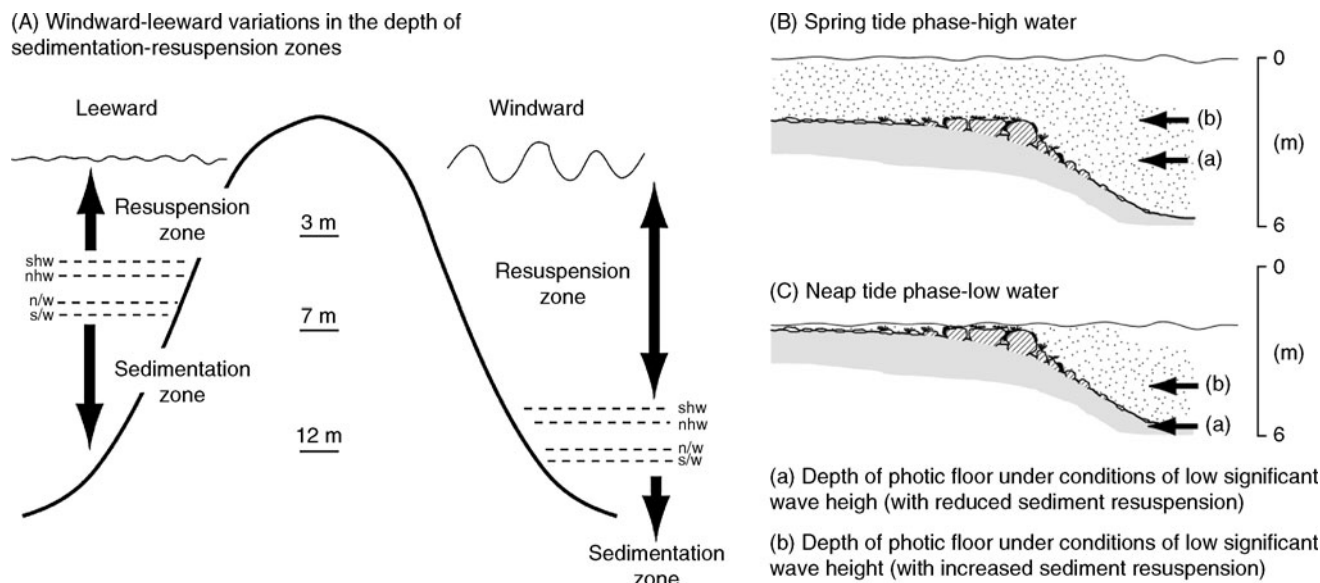
High levels of turbidity, associated either with inputs of fine-grained sediment that are held in suspension in the water column and/or the reworking of seafloor sediments, will primarily impact coral physiology by reducing light levels such that they interfere with algal photosynthesis within the coral tissue. One of the main effects of this is to reduce the depth of the photic zone, effectively raising the “photic floor” (the maximum depth of photosynthesis) so that the depth range for potential reef development becomes bathymetrically constrained. One obvious cause of such high turbidity events is from flood plumes, where large volumes of fine-grained sediment are held in suspension close to the water surface. The extent and duration of these pulsed inputs are clearly dependent upon the magnitude of the flood event, sediment availability within the catchment, and nearshore wave/current patterns that will dictate the spatial extent and mobility of any flood plume. Devlin and Brodie (2005) illustrate the spatial extent of various flood plumes on the Queensland coast, and it is

clear that flood plume distributions vary significantly between events. High-turbidity regimes also result from the resuspension of seafloor fine-grained sediments (originally derived either from riverine inputs or relict lowstand sedimentary deposits), events that have been shown to be strongly influenced by increases in significant wave height (Larcombe et al., 2001). The result of this can be prolonged periods of elevated turbidity regimes that significantly reduce light penetration, thus acting as an important ongoing influence on reef development.

Threshold levels for coral growth under different turbidity regimes are not established and probably vary on a site-by-site and species-by-species basis, but high suspended sediment concentrations (SSCs) have been reported in the vicinity of many inshore reefs along Australia’s Queensland coast. For example, data from sites around Paluma Shoals, indicate that the reefs experience prolonged high turbidity events with recorded SSCs of up to  $175\text{ mg/l}$  and levels  $>40\text{ mg/l}$  estimated to occur for  $>40$  days per year (Larcombe et al., 2001). At Middle Reef, Larcombe et al. (1995) report SSCs in excess of  $5\text{ mg/l}$  for 53% of the time,  $>10\text{ mg/l}$  for 24% of the time, and  $20\text{ mg/l}$  for  $>9\%$  of the time. Much higher SSCs have been identified from long-term temporal datasets from sites around Luggar Shoal where SSCs exceeded  $50\text{ mg/l}$  for  $\sim 55\%$  of the time and  $500\text{ mg/l}$  for  $\sim 19\%$  of the time (SSCs in excess of  $800\text{ mg/l}$  occurred  $\sim 9\%$  of the time) (Whinney, unpublished data). An additional, but significant, point to make in relation to the above is that even given uniform sediment input regimes and seafloor sediment textural characteristics, marked inter and intra-site variations in sedimentation–resuspension regimes will occur depending upon tidal regime and phase (and thus water depth) and degree of exposure to wave energy (see data in Larcombe et al., 2001; Wolanski et al., 2005). As a consequence, the position of the photic floor as well as the threshold depths across which net sedimentation–net resuspension regimes operate will fluctuate markedly through individual and spring-neap tide cycles (Wolanski et al. 2005; see Figure 1).

### A framework model for understanding reef development under conditions of terrigenous sediment accumulation and elevated turbidity

The longevity and magnitude of factors such as terrigenous sediment input, accumulation, and turbidity, as outlined above, clearly interact to control the potential for reef development. On this basis, Woolfe and Larcombe (1999) developed a conceptual framework model within which to consider the controls exerted by these factors on reef-building potential. This conceptual model was based upon a number of key assumptions about coral settlement, establishment, and reef growth with respect to regimes of sediment production, accumulation, and export: (1) that for reef initiation to occur, the rate of terrigenous sedimentation and the rate of reefal production of carbonate must be near zero, because there is no pre-existing reef activity, (2) that immediately after initiation, reefal carbonate production



**Turbid-Zone and Terrigenous Sediment-Influenced Reefs, Figure 1** (A) Spatial and bathymetric variations in zones of net sedimentation and resuspension. Note that the boundary depth between these zones is much lower in leeward settings and also that in both windward and leeward settings the depth of this boundary zone moves vertically (assuming constant wave-energy levels) depending on tidal phase and height (shw – spring tide high water; slw – spring tide low water; nhw – neap tide high water; nlw – neap tide low water). Adapted from Wolanski et al. (2005). (B, C) Hypothetical variations in the depth of the photic floor in turbid-zone reef settings under spring (B) and neap (C) tide phases. Note that the depth of the photic floor will shallow significantly during periods of increased significant wave height, and that it is even possible that during spring high tides the photic floor may be above the surface of the reef flat.

must exceed non-framework sediment accumulation, or young corals will be overwhelmed and buried. This is a valid assumption, although the high volumetric proportion of terrigenous sediments within the basal facies of many turbid-zone reefs suggests that the balance in favor of reefal carbonate production may only be narrow, and (3) that the balance between reefal framework production and non-framework sediment accumulation must remain essentially positive throughout reef accretion.

These assumptions were used to produce a framework diagram based on the relative rates of reefal (framework) carbonate accumulation (R) and non-framework sediment accumulation (T) (Figure 2), within which a field for potential reef accretion can be delineated. These ideas are clearly conceptual in nature, but provide a framework within which the conditions required for turbid-zone reef growth, in the context of regimes of framework accumulation vs. removal, and terrigenous and non-framework sediment accumulation and removal, can be considered.

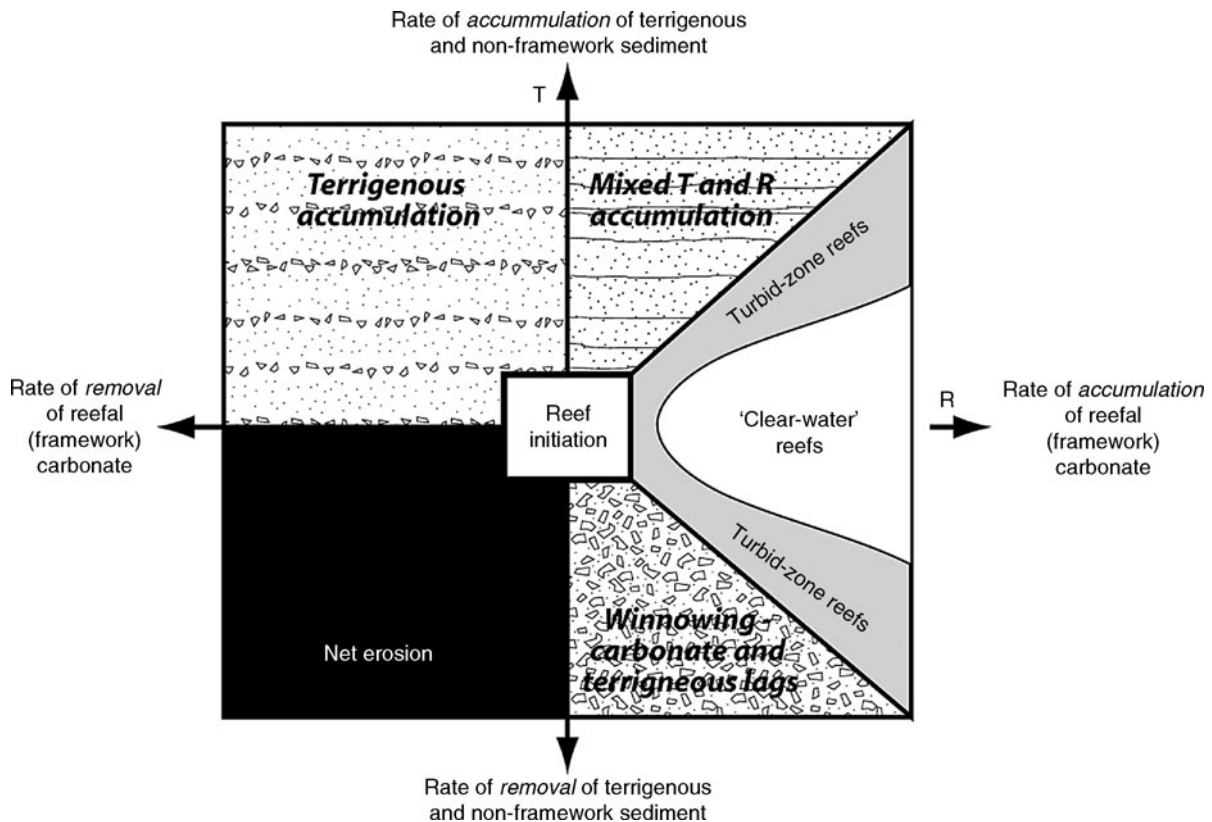
Placing quantitative constraints on the various accretionary and erosional parameters outlined above has not yet been feasible (see Woolfe and Larcombe, 1999 for a discussion), but it is clear that terrigenous sediment inputs and accumulation act not only to control the location and extent of reef development, but also styles of reef development and, within reef environments, reef community zonation patterns. These differences are evident not only at regional scales (see, e.g., Done, 1982), but also over much

smaller spatial scales dictated by proximity to sediment source areas. For example, fluvial inputs of siliciclastic sediments have been shown to control the depth and extent of reef development along the NE coast of Barbados, with reef development becoming more limited with proximity to the point sources of siliciclastic sediment input (Acker and Stearn, 1990), and at sites along natural gradients of terrigenous sediment stress in Puerto Rico where marked shifts in community zonation and coral cover occur along this gradient (Acevado et al., 1989).

### Geomorphic settings and styles of turbid-zone reef development

While terrigenous sediment inputs and/or a legacy of their past input thus exert an important control on coral reef development, it is clear that terrigenous sediment-influenced reefs occur within a wide range of coastal and shallow marine environments, and that reef initiation in these environments can occur above a wide range of sedimentary substrates (e.g., Smithers et al., 2006). In addition, the occurrence of mixed carbonate (reefal): siliciclastic facies in similar settings in the fossil record indicates that such interactions are far from isolated contemporary examples – these fossil reef examples are considered in a detailed review by Sanders and Baron-Szabo (2005). Inevitably, all reefs that develop under conditions of terrigenous sediment influence do so in settings with different shoreline geometries, above a range of sediment substrates and are subjected to varying levels





**Turbid-Zone and Terrigenous Sediment-Influenced Reefs, Figure 2** Framework model of conceptual existence fields for coral reefs in relation to the relative rates of reefal (framework) carbonate (R) and terrigenous and non-framework sediment (T) accumulation. The model delineates fields of net erosion (lower left box) and net accumulation (upper right box). Coral reefs are restricted to the central right hand side of the diagram. Turbidity levels increase away from the x-axis ( $T = 0$ ) associated with either sediment accumulation from turbid water ( $T > 0$ ) or erosion of pre-existing substrates ( $T < 0$ ). "Clear water" reefs plot close to the x-axis and turbid reefs further away. Adapted from Woolfe and Larcombe (1999).

of sedimentation and turbidity influence. Thus, the extent and style of reef-building vary markedly between environments. Three examples below illustrate the diversity of setting, form, and structure that can occur under these varying conditions.

#### Example 1: Muddy, coastal embayment site: South Thailand

Numerous fringing reefs are developed with coastal embayments along the SE coast of Phuket, Thailand, and grow in environments dominated by terrigenoclastic sedimentation (Tudhope and Scoffin, 1994). The main sources of terrigenous sediment are rivers flowing into the semi-restricted Phangnga Bay, and the transport and resuspension of muds results in a strong gradient of turbidity through the bay (underwater visibility ranging from  $<1$  m at innermost bay sites to  $>10$  m outside the bay). Reefs developed in the inner, muddy, and highly turbid areas have reef flats up to 300 m wide and narrow (2–5 m deep) reef fronts, with coral communities dominated by large *Porites* and *Goniastrea* colonies. Much of the internal structure of these

reefs comprises massive, in situ *Porites* and faviid corals, between which a muddy branched coral rubble facies occurs. Radiocarbon dating indicates that reef growth at these sites initiated  $\sim 5,000$  year BP, when sea levels were  $\sim 0.8$  m above present. Reef growth, mostly thorough progradation, has continued to the present, at rates of  $\sim 40$  mm/year. Unusually, reef progradation has been aided by the splitting, toppling, and regeneration of massive reef-front corals – a process driven by the deep boring effects of *Upogebia* sp. shrimp (Tudhope and Scoffin, 1994). The result of reef growth in these settings has thus been the development of laterally extensive, but vertically restricted, reef units above unconsolidated fine-grained terrigenous sands and muds.

#### Example 2: Leeward, barrier island setting: Inhaca Island, southern Mozambique

Narrow fringing reefs and coral communities are intermittently developed along the seaward margins of wide (up to 500 m) intertidal flats that fringe the western (leeward) margins of Inhaca Island, a large siliciclastic sand barrier

island complex, located along the seaward margins of the large estuarine Maputo Bay in southern Mozambique. These shallow nearshore environments are subject to high turbidity levels (which reduce light levels to <5% at depths of ~8 m) and to the effects of periodic smothering and burial of corals associated with a mobile, siliciclastic-dominated sediment substrate (Perry, 2003). These constraints limit coral community development both spatially and bathymetrically, and historical time-scale evidence suggests that the main sites of coral growth presently shift over decadal timescales as a response to periodic sediment remobilization (Perry, 2005). Such rapid rates of turnover restrict the development of rigid framework deposits and, in contrast, the main depositional product of coral growth is branched (mainly *Acropora* sp.) coral rubble – rubble production probably being aided both by intense internal bioerosion (sponge, bivalve, and worm traces) and by periodic storm damage. Much of this rubble accumulates along the margins of the intertidal channels where coral communities are developed and provides a substrate for subsequent coral recruitment. Cores recovered across the present reef-intertidal zone indicate, however, a long-term history of coral community occurrence in this siliciclastic sediment-dominated environment. The internal fabric of the reef comprises a coral rubble floatstone facies dominated by branched coral rubble (often heavily bioeroded, but sparsely encrusted), along with spheroidal rhodoliths and molluscan fragments set within a poorly sorted, mixed siliciclastic:carbonate sediment matrix. Radiocarbon dates indicate that most of the rubble deposits date from the period 6,500–4,700 years BP (Perry, 2005), corresponding to a period of regional sea-level highstand, and which appears to have been a period of rapid reef flat progradation (average progradation rate of around 0.2 m/year). Over the subsequent 4,700 years, progradation of only around 25 m has occurred. This may be attributed to reworking and erosion of the seaward margin of the deposits during periods of fluctuating sea level between 4,700 and 900 years BP, or to a lack of seaward accretionary potential – in this case resulting from significant long-shore current reworking of the accumulating substrate.

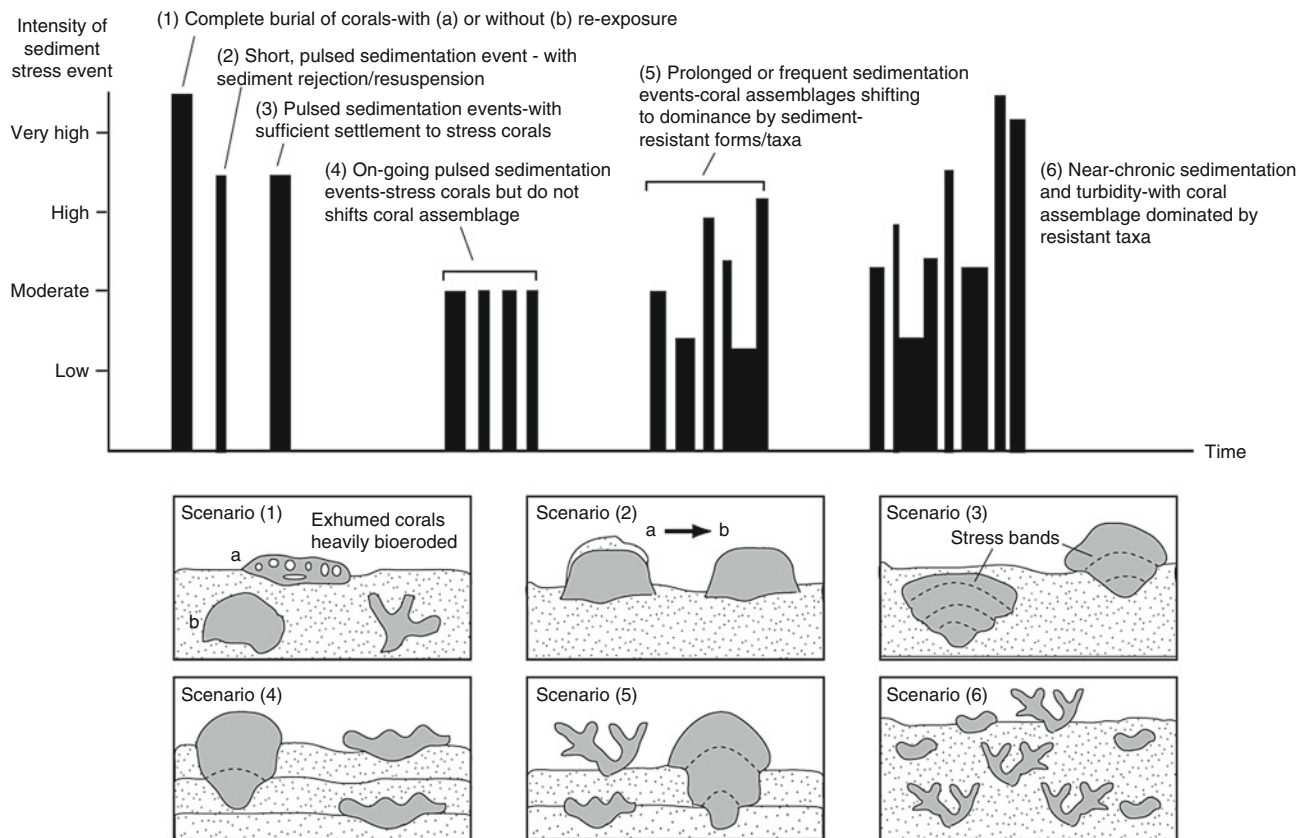
#### Example 3: Open sedimentary coastal setting: Paluma Shoals, inner-shelf, Great Barrier Reef

A number of distinct turbid-zone coral reefs have recently been reported from nearshore sites within Halifax Bay, north Queensland, Australia. Of these, Paluma Shoals is the best documented and occurs in an area with episodically high turbidity levels (SSCs of up to 175 mg/l and levels >40 mg/l estimated to occur for >40 days per year; Larcombe et al., 2001). This results from periods of increased significant wave height and fine-grained sediment resuspension (Larcombe et al., 2001). Paluma Shoals comprises a series of reef flats that are subaerially exposed at lowest astronomical tide level, and two main areas of reef development can be delineated: a northern

shoal complex that is attached on its landward side to wide siliciclastic-dominated intertidal sandflats and a southern shoal that is presently slightly detached (Smithers and Larcombe, 2003). The reefs have developed with this shallow, terrigenoclastic-dominated nearshore environment above a basal Pleistocene clay substrate, with reef growth initiating about 1,600 years BP (Smithers and Larcombe, 2003). These reefs have subsequently grown rapidly to sea level and undergone phases of both seaward progradation and leeward infilling. While the present reef flat surface is dominated by *Porites* and *Goniastrea* bommies, much of the internal fabric of the reef comprises a branched coral rudstone-floatstone, with coral clasts set within a matrix of fine-grained terrigenoclastic sediments. These, and other similar reefs, have developed in a narrow zone of low net sedimentation, but high sediment resuspension, along the very innermost areas of the Great Barrier Reef Shelf. Recent data indicates, however, that similar styles of rapid reef emplacement, under similar turbidity-sedimentary regimes, occurred in this region at different periods through the late Holocene highstand (Perry and Smithers, 2010).

#### Reef facies and framework fabrics in turbid-zone and terrigenous sediment-influenced environments

Data both from the reef sites discussed above, and other types of nearshore settings in which turbid-zone reefs have developed (e.g., Johnson and Risk, 1987; Partain and Hopley, 1989; Kleypas, 1996), highlight the potential for long-term (millennial timescale) persistence of coral communities in settings intimately associated with terrigenous sediment accumulation. Commonly, these reef deposits are characterized by thin sequences of mixed coral rubble and siliciclastic-rich sediment facies. These are distinct from those forming under “clear water” conditions, and there is thus some potential to distinguish these turbid coral communities as distinct forms of fringing reef systems (see also Kennedy and Woodroffe, 2002). The framework facies themselves can be distinguished from those associated with “clear water” reef environments in several ways: (1) by the lack of a rigid reef framework either comprising in-situ coral or encrusted coral rubble, (2) by the distinct lack of rubble encrustation/syn-depositional cementation, and (3) by the predominance of a siliciclastic-rich sediment matrix. The composition and structure of such deposits will, however, depend upon subtle differences in local environmental conditions, e.g., sediment compositions, sediment transport and reworking rates, sedimentation rates and turbidity levels. These are likely to produce a gradational range of depositional environments and as a result a range of “turbid-zone” coral depositional facies that reflect differences in the type, longevity, and magnitude of sediment-related stress events (Figure 3). These differences may be evident either at the community/facies level or at the level of the individual colony.



**Turbid-Zone and Terrigenous Sediment-Influenced Reefs, Figure 3** Conceptual diagram illustrating the impacts of sedimentation events of different intensities and durations on corals and coral communities. Adapted from Sanders and Baron-Szabo (2005).

### Temporal and spatial variations in turbid-zone reef development: a regional perspective based on the Great Barrier Reef Shelf

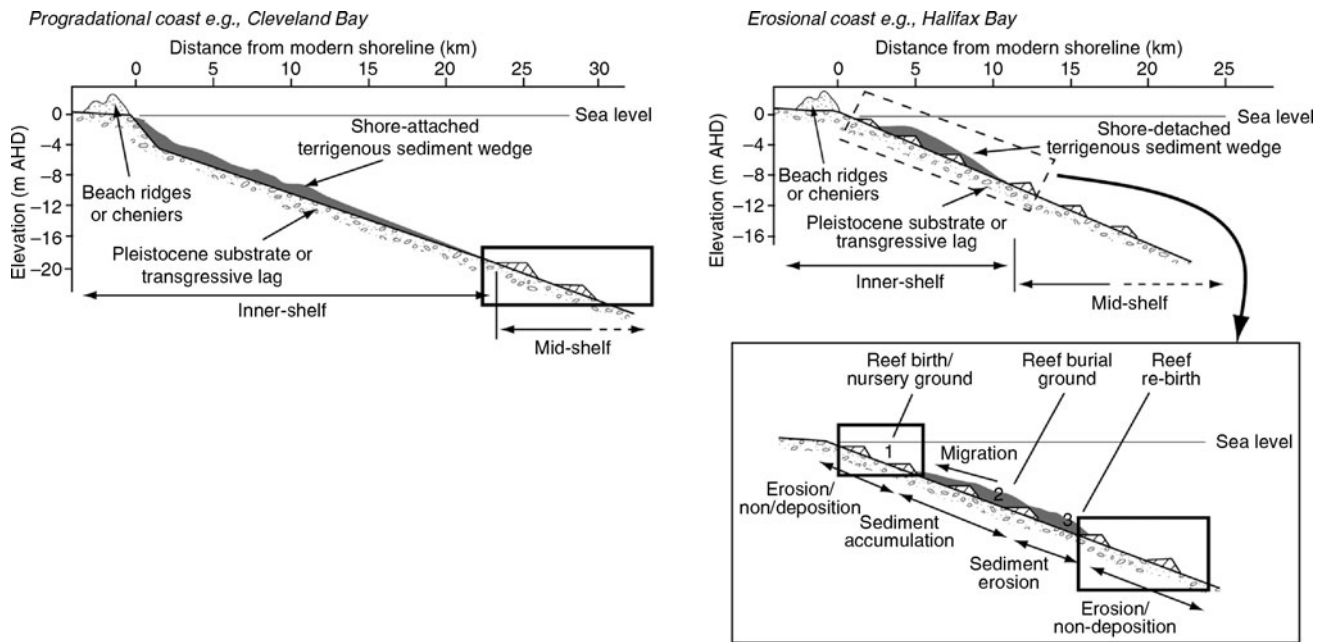
While it is clear that individual turbid-zone reefs can develop within a range of nearshore and inner-shelf locations, and that these clearly demonstrate the potential for reef initiation and growth within terrigenous sediment-dominated inner-shelf environments, it is also useful to consider the nature and influence of large-scale regional terrigenous sediment controls on the location and timing of reef development. This provides a useful insight into turbid-zone reef development on a range of temporal and spatial scales. In this context, the conceptual model developed by Larcombe and Woolfe (1999) that considers the regional location of reef development across the central Great Barrier Reef Shelf provides a useful case study. This model, which was based on assessments of shelf processes, sea-level history, cyclone influence, and sedimentary dynamics on the Great Barrier Reef (GBR) Shelf, Australia, delineated different types of inner-shelf coastline (accretionary and erosional; see Figure 4) and considered the resultant position of the inner-shelf terrigenous sediment wedge as a primary control on reef

establishment. The terrigenous sediment wedge is a body of sediment that accumulated within the inner-shelf areas during the late Holocene transgression and highstand, and it extends out to depths of ~15 m.

Along sections of the coast undergoing net accretion, the sediment wedge is mainland-attached (Figure 4). High net sediment accumulation rates in these areas prevent nearshore reef establishment – and thus, in these areas of the shelf the model suggests that reef accretion is only possible along the inner mid-shelf boundary (i.e., at depth) or around high inner-shelf islands. The existence of reefs along the inner mid-shelf boundary (presumably submerged or relict features) has not been established, but there are a number of examples of reefs that have developed around high inner-shelf islands just within or outside the seaward limits of the terrigenous sediment wedge. These include the reefs described from Fantome Island (Johnson and Risk, 1987) and Pioneer Bay, Orpheus Island (Hopley et al., 1983), which clearly accreted (at least during the early phases of reef development) under terrigenoclastic sediment influence.

In contrast, along erosional coastlines the sediment wedge is mainland-detached (Figure 4), and thus reef growth becomes possible along narrow landward zones of





**Turbid-Zone and Terrigenous Sediment-Influenced Reefs, Figure 4** Conceptual model for inner-shelf turbid-zone reef development on the GBR (adapted from Larcombe and Woolfe, 1999). *Bold boxed* areas highlight the predicted zones in which inner-shelf reef initiation and growth may occur within different coastal sectors.

low net sediment deposition, or again along the inner mid-shelf boundary or around high inner-shelf islands. Several examples of reefs that occur along the mainland coast exist in the literature; some of which are relatively young having initiated and accreted in the last 1–2,000 years, e.g., Paluma Shoals (Smithers and Larcombe, 2003) and Lugger Shoal (Perry and Smithers, 2006), while others established and grew much earlier during the late postglacial transgression and early highstand (e.g., the reefs at Cape Tribulation; Partain and Hopley, 1989). Through the mid-late Holocene sea-level rise and highstand the windows of opportunity for inner-shelf reef establishment and growth, as controlled by the position of the terrigenous sediment wedge, would have changed as the shelf flooded – resulting in marked temporal and spatial variations in reef establishment and accretion potential across the shelf (recently reviewed by Perry and Smithers, 2010). While these ideas have been based upon considerations of the GBR shelf, and have only recently started to be tested in detail, they demonstrate the important influence that long-term patterns of terrigenous sediment accumulation can exert on the location, the timing of, and the potential for, turbid-zone reef development at regional spatial scales.

### Impacts of increased terrigenous sediment yields

While a wide range of environmental and anthropogenic factors have been identified as drivers of late Holocene coral reef community change, elevated sediment (and associated nutrient) yields from anthropogenically modified coastal catchments are commonly implicated. Much of this relates

to the concepts associated with coral-macroalgal phase shifts (see Done, 1992), whereby poor water-quality conditions (including those deriving from high sedimentation and turbidity regimes) may prevent reestablishment of hard coral cover following coral mortality events by promoting a shift to macroalgal dominance. While there is very clear evidence for land-based sediment run-off exerting a very deleterious effect on coral reef “health” (Cortés and Risk, 1985) and rates of reef carbonate production (Edinger et al., 2000) in some areas, the issue is less clear-cut in other regions/sites where clear links between reef community states and water quality changes are complex to establish. At the heart of this lies the very real difficulty in quantifying sedimentation–resuspension–turbidity regimes (discussed above) and the way these parameters interact with coral communities. It is also made difficult by the short timescales over which detailed coral community data, sufficient to allow temporal assessments, are available. In fact, it is perhaps more likely that the nature and magnitude of any community changes and/or patterns of coral community susceptibility, that are directly linked to water quality regime changes, will vary between reef sites and spatially across and along regions, and a number of factors may influence such susceptibility. These include (1) reef proximity to the point-sources of sediment input, (2) the frequency and magnitude of episodic (i.e., flood plume-related) events that can deliver nutrient-enriched waters and suspended sediments to reefs, and (3) perhaps most importantly, the background (or baseline) community structure of the reef (Done et al., 2007). In this final respect a particularly important issue will be the

background environmental conditions under which reef growth has occurred, i.e., the baseline environmental conditions in terms of terrigenous sedimentation (and nutrient) influence to which individual reef communities have adapted during early reef initiation and subsequent growth (see, e.g., the various “impact” scenarios outlined in Figure 3).

While these water quality issues are relevant to many tropical coastlines, the issue has particular high-profile significance to the Great Barrier Reef lagoon, where catchment erosion and fluvial sediment transport rates are reported to have increased markedly since European settlement (from ~1850 AD). Sediment delivery to the inner GBR lagoon is suggested to have increased five- to tenfold since this time (McCulloch et al., 2003), and recent modeling suggests that total nitrogen discharge has increased by a factor of 4, and nitrate and total phosphorus by a factor of 10 (Devlin and Brodie, 2005). The magnitude of these reported and modeled increases has, not surprisingly, raised concerns about the implications for inner-shelf coral reef communities [see Hutchings et al. (2005) and references therein]. However, the extent of any such impacts remains controversial (Larcombe and Woolfe, 1999; McCook, 2001), and debate has persisted, in large part, because long-term (>decadal timescale) coral community data that clearly document temporal community responses under changed sediment or water quality regimes have not, until recently, been available.

However, recent work in this area is starting to provide some perspective on long-term temporal community trends, at least within sites of long-term net terrigenous sediment influence. Perry et al. (2008, 2009), for example, have recently developed millennial timescale records of coral assemblage composition from nearshore sites that have been under fine-grained terrigenous sediment influence throughout their growth history. At these sites, coral community structure appears to have changed little during reef accretion, with the major changes in the presence of reef-building taxa occurring as the reefs have shallowed and reef flats have evolved. A key factor facilitating long-term coral assemblage persistence (stability) at these sites may well be a pre-existing adaptability to deal with the effects of long-term light and sediment “stress” (Stafford-Smith and Ormond, 1992; Anthony, 2000, 2006), with reef building dominated by a few key sediment/light-tolerant taxa. Other records, from other similar sites, are currently being developed and should help to provide a perspective on regional patterns of turbid-zone reef development at different time/space scales. In terms of reef-building potential and in terms of the potential susceptibility of coral assemblages to any changed water quality regime, the most important issue may, therefore, not simply be proximity to the point sources of input, but the composition of the existing coral community and the nature of the pre-existing (baseline) environmental conditions under which reef growth occurred. In more distal (offshore) sites, where contemporary sedimentation–turbidity regimes differ from

those experienced during earlier phases of reef growth the community response patterns may be different – again, this is an area of ongoing research.

## Summary

Recent studies are providing an improved understanding not only of the controls on, but also the dynamic nature of, terrigenous sedimentation, resuspension, and turbidity within nearshore marine environments, and how these parameters fluctuate in and around coral reefs. The key issue that arises from such studies is the need for consideration of the marked variability that occurs spatially (between and across individual reef systems) and temporally (within reef systems/sites). The implications of this are that all turbid-zone and terrigenous sediment-influenced reefs are subject to varying degrees of sediment/turbidity stress. Consequently, the responses exhibited by coral communities and the facies that accumulate are highly site specific. Although the dynamics of sedimentation are often complex, short-term wave-driven sediment resuspension can generate turbidity regimes that far exceed perceived threshold levels for coral survival, while over longer (centennial to millennial) timescales, the landward transgression of inner-shelf terrigenous sediments can control regional patterns of reef establishment.

It is, however, clear that turbid-zone reefs can develop within a wide range of nearshore and coastal depositional environments, with the earliest coral colonizers clearly exploiting a wide range of, often unconsolidated, sediment substrates, including clays, alluvial sands/gravels, and intertidal and subtidal sands and muds (see Smithers et al., 2006; Perry and Smithers, 2009). However, once established, these reefs demonstrate the potential for relatively rapid growth, exhibiting both rapid accretionary and progradational growth modes. Reef facies in these environments typically demonstrate that reef accretion has occurred under conditions of net (often fine-grained) terrigenoclastic sediment accumulation (and are characterized by detrital coral rubble set within a mixed carbonate–siliciclastic matrix). Recent studies also demonstrate that reef building in these environments can be dominated by persistent (but taxonomically restricted) suites of coral taxa, with marked faunal transitions only occurring once the reefs reach sea level and reef flat communities evolve. The long-term tolerance of corals to, at least episodically, high turbidity levels is probably aided by the ability of some corals to switch from predominantly phototrophic to autotrophic feeding modes. These issues are clearly of fundamental importance to understanding the long-term ecological stability of turbid-zone coral reefs and for understanding coral community level responses to sediment flux. Much remains to be learnt, however, about the interactions that occur between reef growth, sea-level fluctuations, and shoreline morphodynamics in these environments, and how these interact to control rates, styles, and the longevity of reef building.

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[Holocene Reefs: Thickness and Characteristics](#)  
[Nutrient Pollution/Eutrophication](#)  
[Postglacial Transgression](#)  
[River Plumes and Coral Reefs](#)  
[Sediment Durability](#)

### **Cross-references**

[Accommodation Space](#)  
[Carbonate Budgets and Reef Framework Accumulation](#)  
[Floatstone](#)

# U

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## UNDERWATER LANDSCAPE MOSAICS

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### Synonyms

2-D mosaics

### Definition

An underwater landscape mosaic is a composite of many overlapping, nadir-view underwater images to form a single large image that provides a “landscape” view of the seabed.

### Introduction

Coral reef ecosystems worldwide are presently threatened by increasing human and natural levels of disturbance (Gardner et al., 2003; Pandolfi et al., 2005; Aronson and Precht, 2006). Current state-of-the-art techniques in coral reef assessment rely on highly trained scientific divers to measure indices of reef health (e.g., substrate cover, species richness, coral size, coral mortality). These indices are commonly derived from line or belt transects, photo-quadrats, or strip video mosaics. Limitations of these approaches include the need to employ highly trained scientific divers/coral reef ecologists, restricted dive time, and spatially inaccurate underwater imagery with a limited footprint. These limitations are addressed by recent advances in underwater landscape mosaic technology (Lirman et al., 2007; Gintert et al., 2009).

A mosaic is a single large image composed of many overlapping images each covering a small portion of the total area. Individual underwater images taken close (~1–2 m) to the seabed have high spatial resolution and minimize water column attenuation but cover only a small area. Mosaics enable a larger area to be viewed in a single

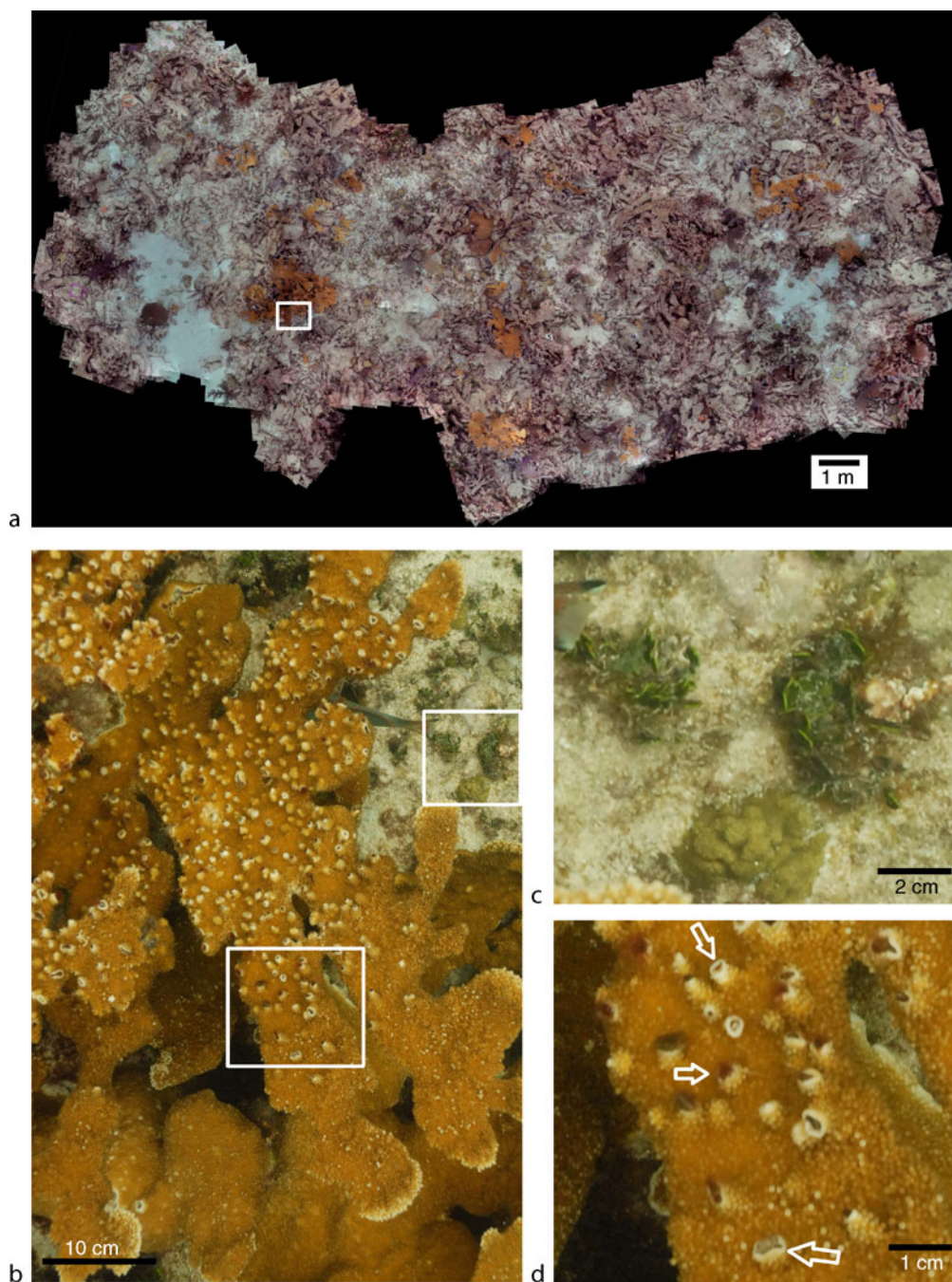
image, thereby not only providing the clarity and resolution of individual pictures but also affording a “landscape view” of the seabed. Near-nadir (downward looking) images are used to create a map-like overhead view of the seabed in which the scale does not vary appreciably across the mosaic.

Current underwater landscape mosaic technology, which uses a combination of video and still images (e.g., Gintert et al., 2009), enables creation of meter-scale maps of reef plots and high resolution images (sub-millimeter-scale) of individual coral colonies (Figure 1). Users can collect imagery for areas of several hundred square meters in under an hour of in-water dive time.

### Background

Pizarro and Singh (2003); Singh et al. (2004); and Ludvigsen et al. (2007) provided brief histories of the development of underwater mosaics. Despite the fact that underwater mosaics have been made for many years, they have not been used routinely for ecological studies until recently for two reasons. First, mosaics have historically required tremendous manual effort to construct, using either physical manipulation of images (Ballard, 1987), digital “photoshopping” (Anonymous, 2001), or interaction with photogrammetric software (Gifford, 1997). Second, imagery used to create underwater mosaics has traditionally been acquired from submersibles or remotely operated vehicles (e.g., Ballard et al., 2002), most often requiring the deployment off acoustic positioning arrays or frames placed on the seabed to guide the camera for data acquisition. Both manual mosaicing and sophisticated underwater engineering are expensive and therefore beyond the reach of the vast majority of coral reef ecologists.

Due to recent advances in technologies, the time is ripe for the application of underwater mosaics to coral reef ecology. Developments in computer vision (Gracias and Santos-Victor, 2001; Gracias et al., 2003; Pizarro and Singh, 2003; Singh et al., 2004) have freed underwater



**Underwater Landscape Mosaics, Figure 1** Underwater landscape mosaic, Carysfort Reef, Key Largo, FL. (a) Mosaic created from video images covers approximately 190 m<sup>2</sup>, with a resolution of 1.35 mm/pixel. Landscape views of meter-scale reef plots are excellent tools for tracking threatened species such as the *Acropora palmata* in this mosaic. (b) Integrated still image (10 megapixel) matched to the boxed area in (a) shows details of individual coral colonies at sub-millimeter scale resolution. (c) Algae and coral, such as the *Halimeda opuntia* and *Porites asteroides* in this enlarged view of the upper box in (b) can be identified to species. (d) Detail of the lower box in (b) showing skeletal chimneys in *Acropora* (arrows) formed as the coral tries to recover from biting by damselfish.

mosaics from the burden of being stitched together by hand. In addition, recent advances in consumer-grade electronics and optics, including cameras, housings, lights, and batteries, mean that high-quality underwater

images do not necessarily need to be acquired by expensive submersibles.

Several researchers have recognized the potential application of mosaicing technology to coral reefs and several



“strip” mosaics of coral reefs have been published (e.g., Kupfner and Lybolt, 2003; Armstrong, 2007; Camilli et al., 2007). These strip mosaics, which are created along transects, lack the spatial accuracy and spatial context of a landscape view of a reef plot (Lirman et al., 2007; Gleason et al., 2007). Other mosaicing efforts, such as by Ludvigsen et al. (2007), used a still camera with very slow frame rates for mosaic creation, necessitating the use of a 400 kg remotely operated vehicle with artificial lights as an imaging platform, and a closed-loop control system that incorporated multiple navigation technologies. Such complex imaging platforms are typically both expensive and unavailable to coral reef biologists.

### Landscape mosaic technology

Landscape mosaic technology allows users to create underwater mosaics with four appealing features for coral reef ecologists (e.g., Lirman et al., 2007). First, processing is automated, converting input video frames to an output mosaic with little to no user intervention. Second, the algorithm is camera and platform independent, requiring only images with a high degree of overlap. Third, the motion model is general enough to deal with unstructured motion including tolerance to moderate off-nadir views. Fourth, the characteristics of the resulting mosaics have been validated against diver data. Areas of  $\sim 400 \text{ m}^2$  ( $\sim 2,000$  frames) can be imaged with sub-millimeter spatial resolution (pixel size) and spatial accuracy of  $\pm 5 \text{ cm}$  (Gintert et al., 2009). Data collection time underwater is less than one hour. Highly automated mosaic production in the lab requires about four man-hours and 24–36 h computer time with current desktop processors. Mosaicing software includes modules for filtering out the effects of refracted sunlight in shallow water imagery (Gracias et al., 2008) and eliminating the visibility of seams among neighboring images in the final mosaics (Gracias et al., 2009).

### Key benefits

Landscape mosaics provide meter-scale views of plots of coral reefs that have previously been unobtainable. This enables new measures of reef health, such as documenting spatial relationships of disease patterns, or the effects of hurricane damage (Gleason et al., 2007) and ship groundings (Lirman et al., 2010). High spatial accuracy, combined with a landscape view, enables accurate size and distance measurements to be taken directly from the mosaic. Mosaics can be georeferenced and integrated with other data sets using Geographic Information Systems (GIS). Mosaics are efficient tools to track patterns of change over time. Mosaics collected in repeat surveys can be referenced to one another with only four permanent markers, allowing monitoring of individual coral colonies without the need for extensive tagging. Due to the ease of data acquisition and relatively short dive times required, landscape mosaics are also superior tools for surveys of mesophotic coral ecosystems (Gleason et al., in press).

The use of landscape mosaics can also reduce the costs of obtaining coral reef and benthic habitat data and improve the quality and archive potential of ecological data. Reduced cost of coral reef monitoring is expected because: (a) special biological training is not necessary for acquiring the imagery; (b) reduced time in the water will increase efficiency of field work, and permit monitoring of deeper sites; and (c) accurate measurement of accidental damage on reefs will minimize restoration costs. For example, effective communication with a jury in a lawsuit following a ship grounding is an example of where this technology could pay for itself. The mosaicing technology is not intended to replace direct expert observations for benthic habitat analysis, but rather mosaics add important capabilities for analyzing, storing, and sharing important time-series data for the purpose of natural resource management. Underwater mosaics both retain the strengths associated with direct expert observations and circumvent the limitations of a traditional diver-only approach.

For additional information see <http://www.rsmas.miami.edu/groups/reidlab/index.html>

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## Cross-references

[AUVs \(ROVs\)](#)  
[Remote Sensing](#)

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## UNVEGETATED CAYS

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On many reef top surfaces there are accumulations of bioclastic, wave and tide transported gravel and sand sized

sediment. Usually, the gravel (shingle) material is concentrated on the windward side of the reef and is a lag deposit whereas the sand sized material is transported to the leeward side of the reef where the refracted waves cause the sediment to deposit about the nodal energy point. The shingle cays tend to remain relatively static in their location except for movement under extreme storm and cyclonic activity. The sand cays are extremely mobile and many are ephemeral. There are recorded instances where sand cays have moved a significant distance across the reef top and in some instances the sediment has been removed from the reef top completely. The previous trace of the existence of such cays is shown by the occurrences of stranded residual beachrock ridges which represent the traces of the previous beach.

The cays develop initially as intertidal banks which build up progressively to be continuously above the high tide level. Many of these cays display the evidence of initial colonization by plants including shrubs. Vegetation may come and go as the upper cay surface is swept by salt-laden moisture in wave run up and washover, especially during cyclones.

The unvegetated cay may evolve over a period of time into vegetated cay which displays serial changes in their vegetation. Such vegetation changes can be reversed by cyclonic damage to the vegetation by wave washover or storm surge.

The unvegetated cays show considerable variety in their shape, size, and orientation with respect to the reef surface. Both elongate elliptical and oval shapes are predominant and the shape usually reflects the shape of the coral reef itself.

Throughout the Great Barrier Reef Province (GBRP) the size of the cays appears to be somehow related to the time that the reef top surface has been exposed to tidal influences. Elongate elliptical and oval shapes occur usually reflecting the shape of the coral reef on which they occur. Throughout the GRBP and also elsewhere in the other reef provinces the size of the cay appears to be related to the length of time that the reef top surface has been at, or near the sea level. In the GRBP, Hopley (1982) identified four types of unvegetated cays. They are:

- (a) Linear sand cays
- (b) Linear shingle cays
- (c) Compact sand cays
- (d) Compact shingle cays

Stoddart et al. (1978) surveyed numerous compact sand cay types in the northern GRBP. Types b. and d. are relatively rare and usually they are unstable. Types, a. and c. are more common. Cays appear to be more prevalent in the inner shelf region of the GRBP, especially the northern GRBP. Unvegetated cays also occur less frequently on the outer barrier ribbon reefs and in the Swain Reef region of the GRBP, however a higher Holocene sea level or even several periods of sea level at or near modern sea level

over a period of several millennia are not a prerequisite for cay development, as coral cays are also common in other reef provinces where sea level is only just reaching current levels, e.g., Belize, Atlantic Reef Province.

The carbon dating of the sediments which constitute the unvegetated cays indicates a mid Holocene to contemporary age (Kench et al., 2005, 2009). This relatively young age is also supported by the young age of the abandoned beach rock ridges, which outline the previous positions of cays that no longer exist or which have migrated to a new position on the reef top surface.

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## Cross-references

[Coral Cay Classification and Evolution](#)  
[Reefal Sediments](#)  
[Vegetated Cays](#)

## UPWELLING AND CORAL REEFS

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### Definition

Upwelling: An oceanographic process where sub-surface water is transported or mixed vertically toward the surface. Upwelling systems usually refer to locations or regions where cool high-nutrient water from the thermocline or below is lifted into the surface layer or euphotic zone, stimulating enhanced biological productivity.

Coriolis force: The deflecting effect of the earth’s rotation on a moving fluid.

### Introduction

Coral reefs are the iconic benthic ecosystem of tropical seas and oceans. The warm, generally clear waters in which most coral reef systems occur are indicative of the low-nutrient (dissolved and particulate) status of these waters and the typically low level of nutrient inputs to these systems. The high productivity of coral reefs is supported by the efficient extraction of dissolved nutrients and organic matter from the very large volumes of water which flow over, around and through reefs, high rates of nitrogen fixation and rapid recycling within reefal food webs. Active reef building does not occur along tropical and subtropical coastlines characterized by strong and persistent upwelling (e.g., Peru, SW Africa), primarily due to low water temperatures (<18°C) in these areas which are below optimal for coral reef growth.

Upwelling occurs when subsurface water moves vertically to replace overlying water which is displaced laterally by a forcing process, usually wind stress on the surface water. Vertical water velocities associated with upwelling are much slower than ocean currents. Horizontal water velocities in ocean currents typically range between  $10^{-1}$  and  $10^2$  cm s<sup>-1</sup>. Average vertical velocities due to upwelling are on the order of  $10^{-4}$  and  $10^{-2}$  cm s<sup>-1</sup>. Upwelling is important in the ecology of the oceans because it returns deep water to the surface. The upwelled water often contains higher concentrations of nutrients which support enhanced phytoplankton production, and in turn, higher levels of herbivores and carnivores: zooplankton, squid, fish, birds, marine mammals.

A close examination of regional coral reef ecosystems indicates that upwelling occurs in many of these systems. The nature of this upwelling differs in a number of ways from upwelling in the larger eastern boundary current and equatorial oceanic divergence zones. Coral reefs can develop where upwelling is less intense or intermittent. The upwelled water rarely reaches the surface to produce the cool surface plumes found in the eastern boundary



current systems (e.g., California, Peru). Rather, the upwelled water is mixed into the low-nutrient surface layer, producing a more diffuse regional enrichment of surface waters. The upwelled nutrients stimulate production of phytoplankton and organic matter in the mixed layer which contributes to regional food chains. Very little of the upwelled nutrients directly impinge on the reefs, and then usually only upon the deeper subsurface part of the reef.

## Upwelling systems and coral reefs

### Topographic upwelling

Currents flowing over and around irregular bathymetry such as seamounts, islands and platform reefs form turbulent boundary zones and 3-dimensional wakes. When surface waters around reefs are drawn into the general flow of the current past a reef, subsurface waters can be upwelled to replace them. One example is the seaward margin of the far-northern Great Barrier Reef (12°S) where a shelfbreak current flows northward past a series of invaginated bays or indentations in the steep shelfbreak reefs. Shoaling of the thermocline has been observed in these invaginations (Thomson and Wolanski, 1984). The shoaling thermocline is characterized by the uplift of the subsurface chlorophyll maximum into the euphotic zone and higher rates of primary production. In shallow continental shelf waters, localized upwelling occurs in eddies formed behind reefs, islands and shoals (Liston et al., 1992).

### Intrusive upwelling

Intrusive upwelling occurs where oceanographic processes raise the oceanic thermocline above the depth of the shelfbreak. The cool, nutrient-enriched waters of the thermocline can then move laterally as a bottom-hugging layer (Andrews and Furnas, 1986). Subsequent mixing on the shelf due to wind stress or turbulence around bathymetry disperses water and nutrients from this layer into the surface layer. Upward movement of the thermocline at the shelfbreak can be caused by a variety of processes, including the offshore displacement of shelf waters by Ekman wind stress which thins the surface layer, uplift of the thermocline in response to geostrophic pressure gradients in ocean currents running along the shelfbreak, internal tides, shelf-waves, or meanders in the shelfbreak current system. Intrusive upwelling associated with boundary currents is known to occur in the central and southern Great Barrier Reef (East Australian Current), on the Campeche Bank, Mexico (Yucatan Current), and along southern and eastern Florida (Gulf Stream).

The timing and extent of intrusive upwelling is variable. Upwelling into the Great Barrier Reef is seasonal, with virtually all occurring during the summer months (October–April). Individual upwelling events (Figure 1) can last for a few days to several weeks. Short-lived events are restricted to the outer continental shelf while episodic large events occurring every few years can extend nearly

across the continental shelf and displace up to one-third of shelf waters (Furnas and Mitchell, 1996). Little is known regarding seasonal or event-coupled variability in Yucatan Current upwelling. During the intrusion events, a bottom layer of Yucatan Channel thermocline water can extend across the Campeche Banks (Furnas and Smayda, 1987). Similar intrusions from the Gulf Stream also occur in the Florida Keys (Leichter et al., 1996) and along the eastern coast of Florida (Atkinson et al., 1978).

The velocity of the shelfbreak boundary current is a major factor influencing intrusive upwelling. Stronger flows are coupled to greater geostrophic tilt of the thermocline. When the thermocline is elevated along the shelfbreak, short-lived shelfbreak events related to internal waves or tides (Leichter et al., 1996) are also more likely to occur.

### Internal waves

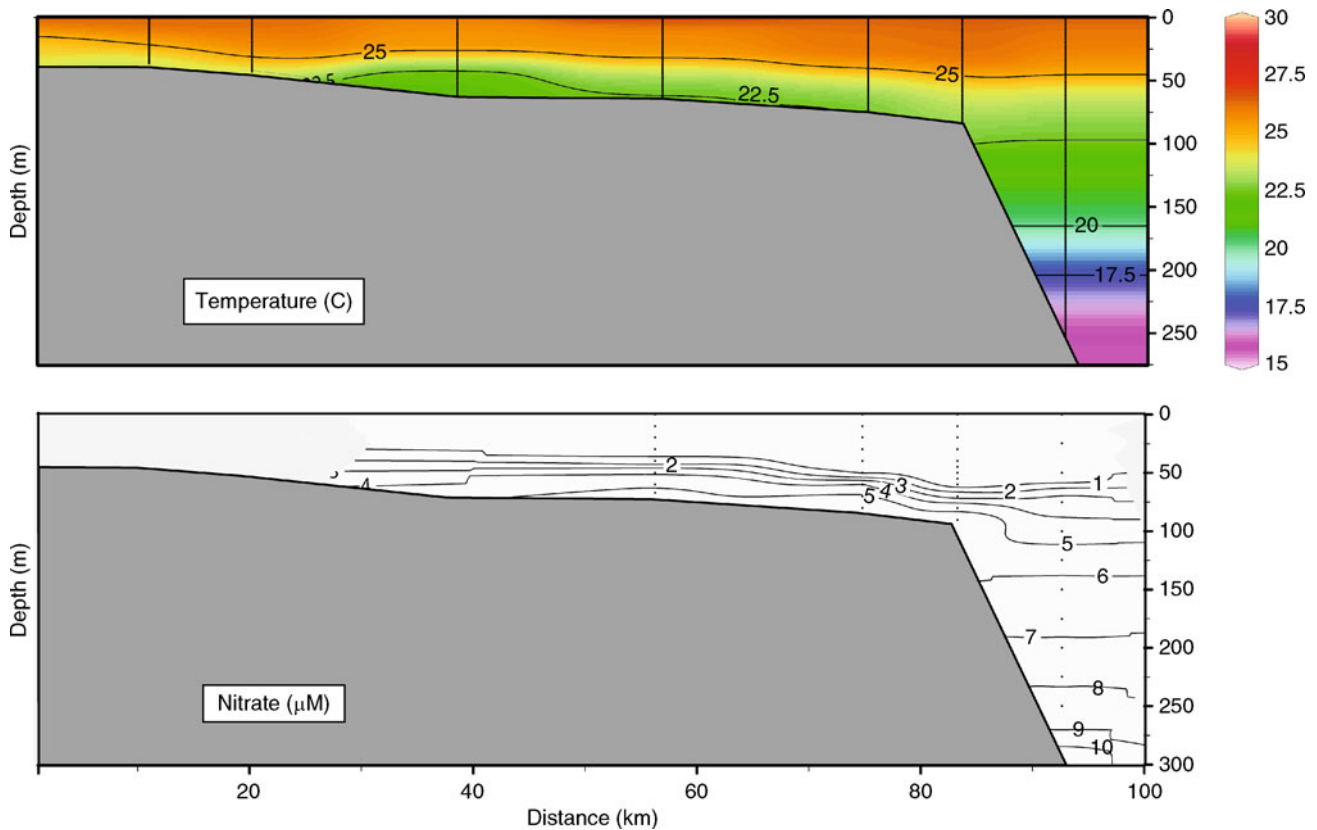
Rhythmic vertical oscillations of subsurface density gradients (internal waves) occur frequently in the ocean. Internal waves are most noticeable at the boundary between the warm (low-density, low-nutrient) surface mixed layer and the thermocline. Internal waves have amplitudes ranging from tens to hundreds of meters and can travel thousands of kilometers across or around ocean basins.

Where the surface layer is relatively thin (<100 m), vertical water movements in internal waves can lift nutrient-enriched thermocline waters and subsurface chlorophyll higher into the euphotic zone where phytoplankton are at least briefly exposed to higher light levels. In situations where the thermocline is shallow enough or waves are large enough, the uplifted high-nutrient thermocline waters can inundate the lower parts of coral reefs with high-nutrient water (Leichter et al., 1998, 2003).

Internal wave interactions with reefs are known from oceanic islands in the Pacific Ocean (Tahiti, Palau; Wolanski and Delesalle, 1995; Wolanski et al., 2004), the Indian Ocean (Scott Reef; Wolanski and Deleersnijder, 1998) and the seaward margin of the Great Barrier Reef (Myrmidon Reef; Wolanski and Pickard, 1983). Where the water movements associated with internal waves interact with local bathymetry, regular vertical density structures can be disrupted, stimulating vertical mixing or transport of nutrients or plankton up the reef slope and into the mixed layer (Leichter et al., 1998).

### Ekman upwelling

Winds blowing over the ocean surface push surface waters downwind. The Coriolis force induced by the rotation of the earth simultaneously deflects the moving water to the right (Northern Hemisphere) or left (Southern Hemisphere). Where winds blow parallel to a coastline and the surface waters are displaced away from the coast, subsurface waters upwell into the surface layer to replace the displaced water. When the upwelled water comes from the thermocline or below, the cooler upwelled water contains higher levels of nutrients which supports higher biological



**Upwelling and Coral Reefs, Figure 1** (Top) Cross-shelf section of water temperature through a cold-water intrusion into Palm Passage, central Great Barrier Reef (18.5°S) in October, 1987. Distances are relative to the inshore end of the transect. The prevailing East Australian Current is transporting water upward out of the page. (Bottom) Concurrent distributions of nitrate in water samples collected on the outer shelf.

productivity. In regions where upwelling is strong and persistent (western North and South America, western North Africa, Namibia) reef growth is inhibited by lower temperatures ( $<18^{\circ}\text{C}$ ) of upwelled water. In some tropical and subtropical locations, however, upwelling-favorable winds are seasonal and warm surface water temperatures persist for much of the year. Examples of intermittent-upwelling systems include the Gulf of Panama (Glynn and Stewart, 1973) and Oman (Glynn, 1993). Wind regimes in these systems are monsoonal with seasonal changes in wind direction that blow surface waters onshore and offshore.

In contrast to South America and South Africa, corals and coral reefs occur along the western side of Australia despite the presence of upwelling-favorable winds for much of the year. Corals are able to grow because upwelling of sub-thermocline water is suppressed by the southward-flowing Leeuwin Current. This current transports warm, low-density water from the Timor Sea southward along the coast. The surface cap of low-density water generally prevents cooler, high-nutrient water from reaching the surface. Wind-forced upwelling does occur, but the upwelled water comes from the low-nutrient

surface layer. A small amount of upwelling of cooler, deeper water occurs episodically along the front of Ningaloo Reef (20°S). Productivity in waters adjoining Ningaloo Reef is higher during El Niño events when flow in the Leeuwin Current is weakened, thinning the surface layer and allowing more deep waters to be mixed into the euphotic zone (Furnas, 2007).

Ekman upwelling also occurs in the equatorial Pacific Ocean where persistent easterly trade winds blow north and south of the equator. Ekman forcing causes surface waters to move away from the equator, creating a divergence zone. The displaced surface waters are replaced by doming subsurface waters along the equator. A number of island systems with coral reefs (Galapagos Islands, Canton Island, e.g., Smith and Jokiel, 1975) are located within the zone of equatorial divergence and resulting high surface-nutrient levels.

### Upwelling and reefal food webs

Upwelling plays an important role in the nutrient biogeochemistry and ecology of the oceans as upwelling returns nutrients to the well-lit surface layer. Regions of active and

persistent upwelling are typically highly productive, both in terms of phytoplankton and higher trophic levels: zooplankton, squid, fish, birds, marine mammals (Ryther, 1969). The high upwelling rates in the major upwelling zones along the eastern margins of ocean basins result in regional water temperatures which are too low for coral growth and reef development.

Coral reefs occur in a number of systems which are subject to either intermittent upwelling or are characterized by hydrographic conditions that largely prevent cold upwelled water from reaching surface-living reefs. The upwelled water is mixed into the surface layer, producing a more diffuse low-level enrichment that supports higher productivity of regional food chains (Furnas, 2007). This productivity produces plankton and particulate organic matter which is accessible to reefal filter and detrital feeders (Hamner et al., 1988). Very little of the upwelled nutrients directly impinge on near-surface reef communities (Andrews and Muller, 1983) to be taken up by benthic algae (free-living and symbiotic).

## Summary

Several types of upwelling processes contribute to the productivity of coral reef systems through low-level or intermittent nutrient enrichment of regional ecosystems without pronounced lowering of water temperatures. Coral reef growth is inhibited in regions of strong and persistent upwelling by suboptimal ( $<18^{\circ}\text{C}$ ) water temperatures. The nutrients introduced by upwelling stimulate regional productivity, which in turn produces plankton and particulate organic matter accessible to reefal detritus and plankton feeders.

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## URANIUM SERIES DATING

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## Synonyms

U-series dating; U-series disequilibrium dating

## Definition

Uranium series: The radioactive decay series that starts with  $^{238}\text{U}$ ,  $^{235}\text{U}$  and  $^{232}\text{Th}$  and ends with stable isotopes of  $^{206}\text{Pb}$ ,  $^{207}\text{Pb}$  and  $^{208}\text{Pb}$ , respectively.



**Secular equilibrium:** A situation in which the quantity of a radioactive isotope remains constant because its production rate (due to decay of a parent isotope) is equal to its decay rate. Secular equilibrium can only occur in a radioactive decay chain if the half-life of the daughter radioisotope is much shorter than the half-life of the parent radioisotope, as typical of the uranium series decay chains.

**Uranium series disequilibrium:** Unequal radioactivity of the intermediate radioisotopes (e.g.,  $^{234}\text{U}$ ,  $^{230}\text{Th}$ ,  $^{226}\text{Ra}$ ) in the U-series decay chains resulting from changes in the respective elemental ratios (or called elemental fractionation) during a geological or environmental event or process. Once disequilibrium occurs, secular equilibrium status will be restored, or in other words, disequilibrium will be reduced to below analytical detection levels, after a period of time, e.g., 5–7 times of the half-life of  $^{230}\text{Th}$  for the  $^{234}\text{U}$ – $^{230}\text{Th}$  disequilibrium.

**Uranium series dating:** A radiometric dating technique is commonly used to determine the age of uranium-rich, mainly carbonate, materials such as speleothem, coral, fossil bone materials, etc. Unlike a U–Pb or Rb–Sr age that is determined by the accumulation of a stable daughter isotope, a U-series age is calculated based on the measurements of the level or degree to radioactive disequilibrium between the parental and daughter radioisotopes (e.g.,  $^{234}\text{U}$  and  $^{230}\text{Th}$ ) within a sample.

## Introduction to uranium series and uranium series dating

$^{238}\text{U}$ ,  $^{235}\text{U}$  and  $^{232}\text{Th}$  (with half-lives of 4.5, 0.7 and 14 billion years, respectively) decay to stable  $^{206}\text{Pb}$ ,  $^{207}\text{Pb}$  and  $^{208}\text{Pb}$ , through the emission of 8, 7 and 6  $\alpha$  particles, and many intermediate  $\beta$  and  $\gamma$  reactions, respectively (see, Ivanovich and Harmon, 1992). The three decay chains involve a total of ten elements (U, Pr, Th, Ac, Ra, Rn, Po, Bi, Pb, and Tl) and 39 isotopes. Half-lives of the 33 intermediate short-lived radioisotopes in these decay chains range from fractions of a second (e.g., for  $^{216}\text{Po}$ ) to 245,000 years (kyr) (e.g., for  $^{234}\text{U}$ ). As such, the uranium series dating technique relies on the decay of these long-lived radioactive uranium and thorium isotopes into a series of unstable, short-lived radioactive “daughter” isotopes. It dates the “event” or “process” that causes elemental or isotopic fractionation leading to radioactive disequilibrium among the intermediate short-lived radioisotopes. As the majority of these short-lived radioisotopes have half-lives ranging from a few hundred thousand years down to only a few years, the method provides a dating range for the different uranium series of a few thousand years to 500,000 years (i.e., seven half-lives of  $^{230}\text{Th}$ ). Uranium series have been used to date uranium-rich mineral deposits, deep-sea sediments, shells, bones, and teeth, and to calculate the ages of ancient lake beds.

Among a large number of the intermediate parent–daughter disequilibria, only the  $^{238}\text{U}$ – $^{234}\text{U}$ – $^{230}\text{Th}$  disequilibrium is most commonly used for palaeoenvironmental applications, such as dating reef corals

and speleothems. The companion low-abundance  $^{235}\text{U}$  to  $^{207}\text{Pb}$  decay chain via  $^{231}\text{Pa}$  (half-life, 32.7 kyr) is seldom used, because Pa occurs in large quantities only in uranium ores; its geochemical characteristics are difficult to determine, and its measurement is analytically challenging. Nevertheless,  $^{235}\text{U}$ – $^{231}\text{Pa}$  disequilibrium has found some applications in coral dating and palaeoceanography, especially for assessment of the coral age reliability in combination with the  $^{234}\text{U}$ – $^{230}\text{Th}$  disequilibrium (Edwards et al., 1997).

## $^{238}\text{U}$ – $^{234}\text{U}$ – $^{230}\text{Th}$ disequilibrium dating or U–Th dating: theoretical principle

Here, only  $^{238}\text{U}$ – $^{234}\text{U}$ – $^{230}\text{Th}$  disequilibrium dating [also commonly described in literature as Uranium–thorium (U–Th) dating, Thorium-230 dating,  $^{238}\text{U}$ – $^{234}\text{U}$ – $^{230}\text{Th}$  disequilibrium dating,  $^{238}\text{U}$ – $^{230}\text{Th}$  disequilibrium dating, U-series disequilibrium dating and U-series dating], which is most relevant to coral reef studies, will be described in detail.

As described above, the U–Th dating method is based on the decay of  $^{238}\text{U}$  (with a half-life  $T_{1/2} = 4.469 \times 10^9$  years) to stable  $^{206}\text{Pb}$  via intermediate daughters such as  $^{234}\text{U}$  ( $T_{1/2} \sim 245,000$  years) and  $^{230}\text{Th}$  ( $T_{1/2} \sim 75,400$  years). In this decay series,  $^{238}\text{U}$ – $^{234}\text{U}$ – $^{230}\text{Th}$  disequilibrium occurs when U is differentiated from Th during a particular geological or environmental event or process. In the case of natural aqueous systems, for example, in which U is slightly soluble, but Th is highly insoluble, carbonate precipitated from the aqueous system will contain trace amounts of U (usually 0.01–100 ppm), but virtually no Th, leading to excess U in the decay chain (that is,  $^{238}\text{U}$  and  $^{234}\text{U}$  activities  $\gg$   $^{230}\text{Th}$  activity). Once this radioactive disequilibrium is established, it takes about seven times the half-life of  $^{230}\text{Th}$  ( $\sim 500$  kyr) for the system to return to near secular equilibrium, or to the level where the degree of disequilibrium is below the limit of detection by thermal ionization mass spectrometry (TIMS) or inductively-coupled plasma mass spectrometry (ICP-MS). The application of  $^{238}\text{U}$ – $^{234}\text{U}$ – $^{230}\text{Th}$  systematics allows accurate age determinations spanning the last 500,000 years, covering  $\sim$ seven times the half-life of  $^{230}\text{Th}$ . For samples that contain U and small to negligible amount of Th, the ages are determined from the following simplified equation (modified after Edwards et al. (1987a) :

$$1 - \left( \frac{^{230}\text{Th}}{^{238}\text{U}} \right) = e^{-\lambda_{230}T} - \left[ \left( \frac{^{234}\text{U}}{^{238}\text{U}} \right) - 1 \right] \times \left( \frac{\lambda_{230}}{\lambda_{230} - \lambda_{234}} \right) \left( 1 - e^{(\lambda_{234} - \lambda_{230})T} \right),$$

where  $(^{230}\text{Th}/^{238}\text{U})$  and  $(^{234}\text{U}/^{238}\text{U})$  are the measured activity ratios, and  $\lambda_{230}$  and  $\lambda_{234}$  are the decay constants of  $^{230}\text{Th}$  and  $^{234}\text{U}$ , respectively, and  $T$  is the age of the sample, which can be worked out iteratively.

The validity of the age calculated from the above equation relies on a number of assumptions: (1) the U–Th

isotopic systematics remain closed since the formation of the dated material or, in other words, since the U/Th fractionation event; (2) the generation of the dated material is a fast process relative to the time elapsed since, so that this process can be considered as a U/Th fractionation “event;” and (3) the dated material does not contain any initial inherited  $^{230}\text{Th}$  at the time of formation, or this initial  $^{230}\text{Th}$  is small or precisely known and can be corrected for. The correction of initial or non-radiogenic  $^{230}\text{Th}$  is based on the measurement of  $^{232}\text{Th}$  presented in the sample and the assumption of initial  $^{230}\text{Th}/^{232}\text{Th}$  ratio. Usually, a bulk Earth  $^{230}\text{Th}/^{232}\text{Th}$  ratio of  $4.4 \times 10^{-6}$  with arbitrarily assigned 50% is used for correction and this assumption holds in most cases (Shen et al., 2008). However, recent studies show that such ratios may vary dramatically in some corals and speleothems (Beck et al., 2001; Cobb et al., 2003; Hellstrom, 2006), and thus site-specific initial ratio measurement is needed for high-precision dating especially for very young corals (Shen et al., 2008; Yu et al., 2006).

### U-Th dating: analytical methods

Bateman (1910) first proposed that the U-series can be used for dating. Khlapin (1926) first applied the U-series to dating uranium-rich minerals (e.g., uraninite) assuming that these minerals do not contain initial Th and  $^{238}\text{U}$  and  $^{234}\text{U}$  are in secular equilibrium. Barnes et al. (1956) first applied the  $\alpha$ -counting method to dating corals. Chen et al. (1986) performed the first precise analysis on  $^{234}\text{U}$  in seawater using TIMS. Edwards et al. (1987a) made the first  $^{230}\text{Th}$  measurements in corals by TIMS. Luo et al. (1997) first used multi-collector ICP-MS to measure U and Th isotopes.

The  $\alpha$ -counting method, or called alpha spectrometry, is based on measuring  $\alpha$  particles of specific energy emitted from U and Th isotopes of a sample. The mass spectrometry techniques directly measure U and Th isotope ratios in a sample. Prior to alpha- or mass- spectrometry measurements, the sample is dissolved and doped with a tracer or called spike consisting of a mixture of artificially enriched  $^{229}\text{Th}$  (or  $^{228}\text{Th}$ ) and  $^{233}\text{U}$  (and/or  $^{236}\text{U}$ ) with known concentrations. Then, U and Th in the sample are pre-concentrated, separated and purified using established chemical procedures including ion exchange chromatography. Through measuring the mixed isotope ratios by alpha or mass spectrometry, U and Th concentrations and isotope ratios in the sample are calculated and then the sample age worked out using the above equation.

Comparing with  $\alpha$ -counting, the mass spectrometry U–Th dating techniques offered great improvements in precision with an order of magnitude reduction in sample size and measurement time. There are now three different mass spectrometry techniques that are in common use for U-series dating: thermal ionisation (TIMS) (Edwards et al., 1987a), inductively coupled plasma (ICP) ionisation using a sector magnet and a single collector system (SC-ICP-MS) (Shen et al., 2002), and ICP ionisation using

a sector magnet and a multi-collector system (MC-ICP-MS) (Luo et al., 1997). In all instruments, the radioisotopes of interest are ionised, separated according to mass and detected using either Faraday collectors or ion counters in analog or ion-counting mode. ICP-based systems achieve nearly complete ionisation of all elements and have orders of magnitude better sensitivity than TIMS systems for U and Th which both have high ionisation potential. However, sampling of the plasma by the mass spectrometer is only about 1% efficient, and instrumental mass-dependant isotope fractionation affects ICP-based systems an order of magnitude more strongly than TIMS. Because of this, MC-ICP-MS offers only a moderate advantage over TIMS, and TIMS analysis is expected to find continued use for some time into the future. MC-ICP-MS is clearly superior to TIMS in sample throughput (e.g., Hellstrom, 2003) and in achieving high-precision dating for samples beyond 300 kyr because Th mass fractionation can be monitored and corrected (Stirling et al., 2001). TIMS is still more commonly used in dating extremely young carbonates, especially corals (e.g., <1,000 years) (Zhao et al., 2009, for review).

In addition, the development of laser ablation techniques allows in situ U–Th analysis of uranium-rich samples to be performed on the MC-ICP-MS, offering new dimensions of applications (Eggins et al., 2005; Potter et al., 2005; Stirling et al., 2000). More recently, an order of magnitude improvement in precisions was achieved on the MC-ICP-MS by measuring all the isotope signals on Faraday collectors with high concentrations of U and Th, enabling coral and speleothem samples of more than 300 kyr to be precisely dated (Andersen et al., 2004).

### U-Th dating: applications

Since the development of mass spectrometry techniques over 20 years ago, U–Th dating has found widespread applications in the fields of geological, environmental and archaeological sciences, revolutionized Quaternary research. Comprehensive descriptions of the techniques and major applications can be found in key text books such as Ivanovich and Harmon (1992) and Bourdon et al. (2003) and some review articles (Edwards et al., 2003; Goldstein and Stirling, 2003; McDermott, 2004; Schwarcz, 2002; van Calsteren and Thomas, 2006; Zhao et al., 2009). The applications of U–Th dating to coral reef studies are discussed in detail in a great volume of literature (e.g., Bard et al., 1990a,b, 1996; Chen et al., 1991; Edwards et al., 1987a,b; Potter et al., 2005; Scholz and Mangini, 2007; Shen et al., 2008; Stirling et al., 1998; Thompson and Goldstein, 2005). Examples of important outcomes from such studies include accurate calibration of  $^{14}\text{C}$  timescale beyond the range of dendrochronology (Bard et al., 1990b; Schramm et al., 2000; Beck et al., 2001), precise timing and characterisation of glacial–interglacial cycles up to 500 kyr BP (Winograd et al., 1992, 1997), establishment of the duration of the last interglacial sea-level high stands (Edwards et al., 1997;

Henderson and Slowey, 2000; Stirling et al., 1995, 1998), characterisation of sea-level fluctuations during the last glacial–interglacial cycles (Bard et al., 1990a; Chappell et al., 1996; Esat et al., 1999), recognition of leads and lags in global climatic oscillations and sea surface temperature changes (Beck et al., 1997), and dating and characterisation of global monsoon variability and calibration of the Greenland ice core chronology (Wang et al., 2001, 2004, 2005, 2008; Yuan et al., 2004).

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## Cross-references

[Electron Spin Resonance Dating \(ESR\)](#)  
[Last Interglacial and Reef Development](#)  
[Postglacial Transgression](#)  
[Reef Structure](#)

# V

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## VANUATU

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### Introduction

Vanuatu is an archipelago located in the South-West Pacific (Figure 1) composed of numerous volcanic islands. These islands are part of the Vanuatu island arc located at the convergent boundary of the Australian and Pacific tectonic plates (Figure 1). The central part of this island arc is characterized by the absence of a physiographic trench because of the subduction of morphological features from the d'Entrecasteaux zone and by the unusual proximity of the island of Espiritu Santo and Malakula close to the plate boundary. Moreover, the islands are surrounded by modern reefs and most of them are characterized by emerged reefs (Figure 2) and a series of raised coral terraces. The Holocene uplift rate of the islands of the central part reaches up to  $5.5 \text{ mm} \cdot \text{year}^{-1}$  in the southwest of Espiritu Santo and up to  $3.4 \text{ mm} \cdot \text{year}^{-1}$  in the north of Malakula (Taylor et al., 1980, 1987). The occurrence of three parallel chains, viz., the western chain (Espiritu Santo and Malakula), the central chain (active volcanoes of Aoba and Ambrym) and the eastern chain (Maewo and Pentecost), is also uncommon as noted by Mitchell and Warden (1971). The distribution and consequently the extension of modern reefs depend on the tectonic history and the sea-level variations.

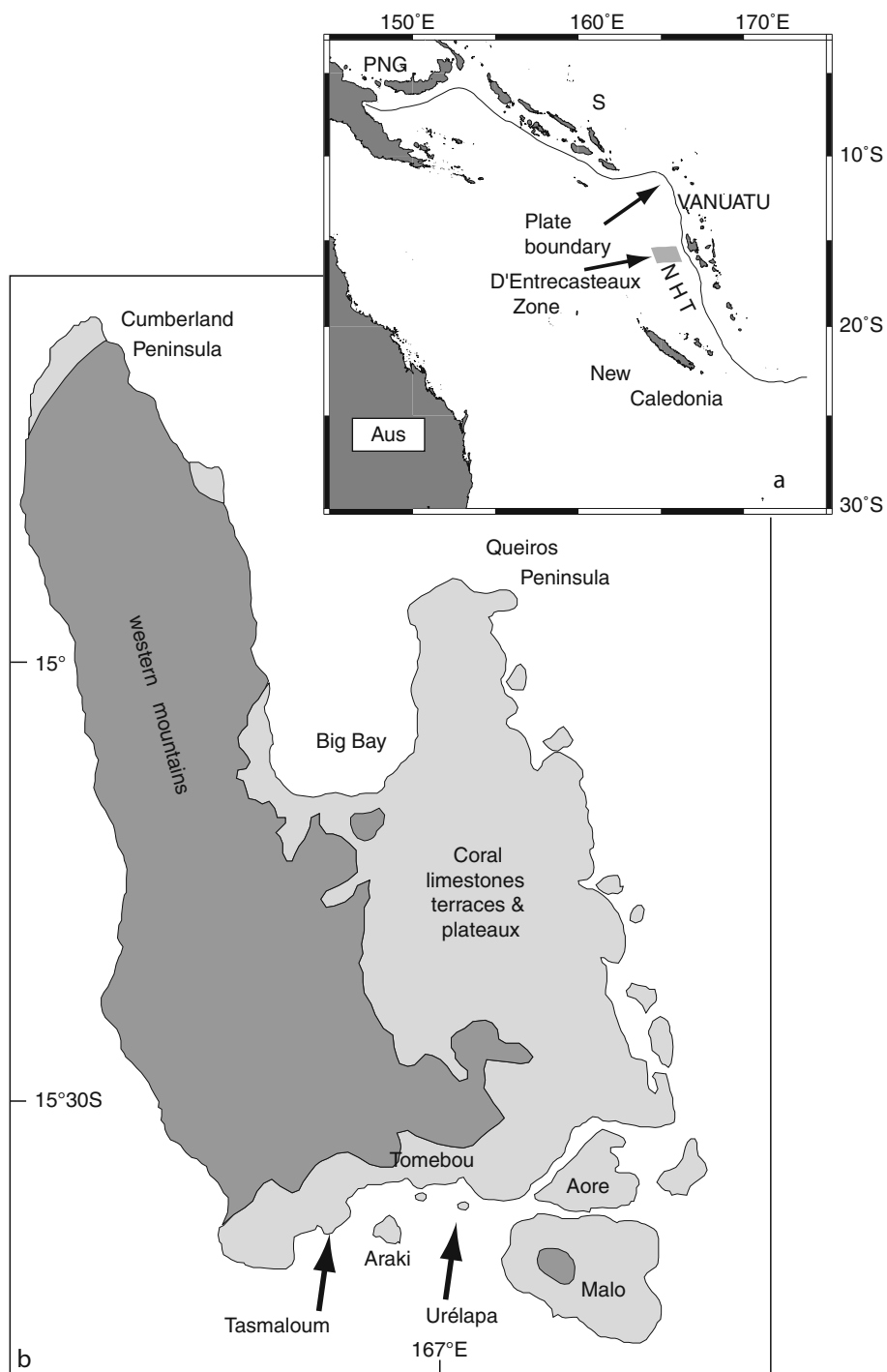
### The modern reefs

Although little is known regarding the morphology and biology of the Vanuatu reefs, some studies were previously performed. Guilcher (1974) analyzed the structure and defined different types of reefs comprising the fringing and open-sea reefs. In 1990, Veron identified 62 genera

and about 296 species of reef corals and Done and Navin (1990) defined different and typical shallow water habitats of many coral reefs around several islands. This last study revealed differences in the zonation of assemblages between exposed and sheltered reefs. In the outer reef slopes, the biological communities are characterized on the reef crests by abundant coralline algae and robust-branching corals (mainly *Acropora* spp. and pocilloporids) and in the reef slopes by massive and branching corals. The open embayments are characterized by massive domal *Porites* spp. accompanied by *Acropora* spp. while the sheltered embayments by soft corals sometimes with domal *Porites* spp. and various branching forms of corals.

### Neotectonics and sea-level variations

Coral reefs can be used as recorders of neotectonic movements and paleosea level (Figures 2 and 3) as reported by the numerous works performed on the raised reef terraces from Vanuatu by Mitchell (1968), Neef and Veeh (1977), Jouannic et al. (1980, 1982) and Taylor et al. (1980). Moreover, all these works show the broad potential of this area to analyze in detail the Late Quaternary sea-level variations. In Vaté, identification of sea levels from the last 125 ka (1 ka = 1,000 years) was performed by Neef and Veeh (1977). In Malakula, previous surveys identified six main terraces in the North West culminating up to 350 m (Mitchell, 1968; Jouannic et al., 1980). More recent U/Th coral dating of a series of raised terraces provides sea-level estimates of the marine isotopic stage (MIS) 3 and several higher relative sea levels were identified from 55 to 40 ka (Cabioch and Ayliffe, 2001). North of Malakula, the island of Espiritu Santo is characterized by a series of raised terraces in the east and south and on islands off the south coast including Aoré, Malo, Araki, Tangoa and Urélapa Islands (Jouannic et al., 1980; Taylor et al., 1980, 1985, 1987, 2005). The altitude of coral terraces increases to the west indicating a tilting to the east.



**Vanuatu, Figure 1** (a) the South-West Pacific showing the plate boundary and the location of the Vanuatu archipelago. AUS: Australia; PNG: Papua New Guinea; S: Solomon Islands; NHT: New Hebrides (Vanuatu) Trench. (b) location of the coring sites in the island of Espiritu Santo at Tasmaloum and Urélapa.

Coral dating in terraces and cores performed in the sites of Tasmaloum and Urélapa (Figure 1) shows the occurrence of a Late Quaternary cycle of uplift and subsidence in Espiritu Santo over one or two hundred thousand years

(Taylor et al., 2005). This cycle can be explained by the subduction of morphological features on the D'Entrecasteaux Zone on the converging Australian plate (Figure 1).





**Vanuatu, Figure 2** Example of emerged reefs in Vanuatu because of the uplifting (photo G. Cabioch/IRD).



**Vanuatu, Figure 4** Emerged Holocene coral on an uplifted reef (photo G. Cabioch/IRD).



**Vanuatu, Figure 3** Modern corals observed just below the sea surface (photo G. Cabioch/IRD).

In addition at the scale of the Holocene, modern emerged corals and reefs (Figures 2 and 4) were used to analyze the recent vertical motions especially to estimate the uplift rate and the seismic recurrence intervals and the timing of aseismic subduction in the central part of Vanuatu (Taylor et al., 1980, 1985, 1987, 1990).

### Paleoclimatology

Corals from Vanuatu offer the opportunity to study the climatology of the past using the isotopic analyses and/or trace element measurements. The variations of isotopes and trace elements (Sr/Ca, U/Ca) document the variations of the past sea surface temperatures (SST) and sea surface salinities (SSS). In 1997, the analyses of *Porites* corals collected in cores from Espiritu Santo by Beck et al., and dated at 4228, 9550, 9731 and 10344 year BP, indicate SST close to present for the 4,228-year-old *Porites*, and 5–7°C cooler

prior to that time for the others. This work was one of the first studies related to the evolution of the SST during the last deglacial sea-level rise. Parallel to such studies, Vanuatu, south of the West Pacific Warm Pool, is located in a region affected by the climatic interannual variations due to the El Niño Southern Oscillation (ENSO) phenomenon and the Vanuatu can be considered as a key region to analyze its frequency and intensity using coral analyses. In this region, the fluctuation of the south branch of the Intertropical Convergence Zone, the South Pacific Convergence Zone, is marked by variations in the oceanographic parameters. Several works were devoted to this topic. The  $\delta^{18}\text{O}$  analyses of a 173-year-old coral by Quinn et al. (1996) document the climatic variability at Espiritu Santo. These analyses show the combined effects of SST variations and rainfall (SSS changes). In 2004, Kilbourne et al. evaluated various methods to reconstruct the SSS in Espiritu Santo on a *Porites* coral and concluded that combining  $\delta^{18}\text{O}$  and Sr/Ca measurements is a reliable tool to reconstruct the SSS. In 2000, Corrège et al. measured the SST in a 47-year-old *Porites* coral dated at 4,166 cal year BP. Comparison between the SST from this fossil coral and the modern instrumental SST revealed cooling anomalies of SST, interpreted as reflecting more intense El Niño events (see entry *El Niño, La Niña, and ENSO*) and a stronger interannual variability at this period. In 2004, Corrège et al. analyzed a *Diploastrea* coral from the Younger Dryas providing data on this peculiar period.

### Radiocarbon calibration and reservoir ages

The corals from Vanuatu appear to be of broad interest to contribute for the extension of the radiocarbon calibration curve and the knowledge of the reservoir ages. In 1998, Burr et al. performed both radiocarbon and  $^{230}\text{Th}$  analyses for  $^{14}\text{C}$  calibration with decadal resolution on a *Diploastrea heliopora* coral from the Younger Dryas (between 11.7 and

12.4 cal ka BP.) of Espiritu Santo. The data show sporadic rapid increase in the  $\Delta^{14}\text{C}$  in relation with the climatic changes during this period of the Younger Dryas. In 2004, Cutler et al. calibrated radiocarbon dates (between 8 and 23 ka) with  $^{230}\text{Th}$  and  $^{231}\text{Pa}$  measurements performed on the corals of Espiritu Santo. Then, in 2005 Chiu et al. (2005) performed high-paired  $^{230}\text{Th}/^{234}\text{U}/^{238}\text{U}$  and  $^{14}\text{C}$  measurements on corals from Araki island extending the calibration curve from 12 to 50 ka. Taking into account these results, a statistical model was proposed to estimate the conversion of ages obtained using radiocarbon into calendar years. More recently, a work dedicated to the analysis of the reservoir ages from the Younger Dryas, covering 700 years, showed that the average was larger than today and a reservoir age variability on a decadal timescale (Burr et al., 2009).

### Reef development during the last 24 ka of the deglacial sea-level rise

Several coring operations were performed in the uplifted reefs of 2 areas of Espiritu Santo at Tasmaloum and Urélapa (Figure 1) characterized by uplift rates of about  $5.5 \text{ mm}\cdot\text{year}^{-1}$  and  $3 \text{ mm}\cdot\text{year}^{-1}$ , respectively (Taylor et al., 1980). At Tasmaloum, several episodes of development can be observed from 24 to 15 ka with fine skeletal detrital facies and robust-branching corals, then from 15 to 10 ka with dominant robust branching coral assemblage indicating another shallowing up sequence and from 10 to 6 ka, a mixture of robust branching coral and foliaceous coral assemblages typical of deeper waters, probably reworked. Moreover, microbialite crusts can be observed from 20 to 6 ka, and particularly abundant from 16 to 10 ka (Cabioch et al., 1998). At Urélapa, a small uplifted island, the reef development is characterized by two episodes well marked by the composition of corallgal assemblages. The first episode, from 23 to 11.5 ka, is characterized by assemblages characteristic of medium to high energy conditions close to the sea surface (keep-up mode) while the second episode from 11.5 to 6 ka by corallgal assemblages of relatively deeper habitats from 10 to 20 m. The succession of these two episodes of corallgal assemblages from a keep-up growth to a catch-up growth mode  $\sim 11.5$  ka probably indicates global plaeoceanographic changes (Cabioch et al., 2003). Such studies show that the analyses of corallgal biofacies provide useful information to analyze the history of the reef development and to examine the role of global (or regional) oceanographic factors and tectonic parameters on reef growth.

### Summary

The distribution of coral reefs of the Vanuatu archipelago and the occurrence of coral terraces depends on the tectonic factor in this area of island arc. Nevertheless, the reef development, although disturbed by this factor, appears to be controlled by global climatic factors. This is well illustrated by the occurrence of growth mode change at  $\sim 11.5$  ka. The occurrence of successive coral terraces is also under the control of the eustatic sea-level variation in combination

with the vertical motions. The climatic context of the region of Vanuatu, located in the zone of fluctuation of the SPCZ is of broad importance. Consequently, high monthly resolution geochemical analyses of corals provide information on past SST and SSS giving data on the past ENSO phenomenon.

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[Earthquakes and Emergence or Submergence of Coral Reefs](#)  
[El Niño, La Niña, and ENSO](#)  
[Emerged Reefs](#)  
[Fringing Reefs](#)  
[Holocene Reefs: Thickness and Characteristics](#)  
[Last Glacial Interstadials](#)  
[Pacific Coral Reefs: An Introduction](#)  
[Paleoclimate from Corals](#)  
[Postglacial Transgression](#)  
[Sea Level Change and Its Effect on Reef Growth](#)

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## VAUGHAN, THOMAS WAYLAND (1870–1952)

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Thomas Wayland Vaughan (1870–1952) was a pioneering paleontologist who made major contributions to the systematics and ecology of living and fossil corals, to coral reefs, larger foraminifera and Tertiary stratigraphy of Florida and the entire West Indies.

As a youngster during the turn of the century in a small East Texas town, he collected fossil plant impressions. That interest in paleontology flowered later as a student at Harvard where he became interested in fossil corals. After a year of studying specimens in Europe's museums he began what was to be a thorough characterization of the Tertiary and living corals of the Americas. His first publication in 1900 was a landmark monograph on Eocene and Lower Oligocene corals of the United States that established him as an authority on the systematics of hexacorals. Next, he shifted emphasis to a study of extant corals of Hawaii and Laysan. By 1907 he had completed the first comprehensive analysis of that fauna, a publication that is notable for its assembly of all available ecological data. The many questions raised by his works on coral skeletons, made Vaughan realize that the answers could only come from a study of living corals.

Beginning in 1907 and for more than a decade he spent parts of every summer researching living corals mostly at the Carnegie Institute's Tortugas Marine Laboratory on remote Loggerhead Key some sixty miles west of Key West, Florida. There he began summer research on the ecology of corals and on the coral reefs of Florida and the Bahamas. Among his accomplishments were the first systematic data on growth rate of reef-building corals of the Tropical North Atlantic, the ecology of coral reefs in Florida and the Bahamas and much more. During the rest of the years from his base in Washington he led the exploration of the Cenozoic geology of Florida and eventually of most of the islands of the West Indies and the Panama.

Always quick to publish his findings, Vaughan produced dozens of substantial works on the geological history of corals and coral reef limestones. In addition he authored seminal works on calcareous sediments and the first geological history of southern Florida. Vaughan's final contribution to the coral literature was his collaboration with John Wells that produced a still-consulted 1949 monograph on corals of the tropical Atlantic.

At the age of 52 he shifted his scientific interests to the larger foraminifera and became a leader in that specialty just as he had done for corals and coral reefs. After 30 years as a member of the United States Geological Survey, he left in 1924 to be Director of the Scripps Institution for Biological Research. For the next dozen years he led the development of Scripps' graduate training and its expansion into oceanographic research. For much of that period he also chaired two influential committees one on international Pacific oceanography and the other on submarine configuration of the oceans. Oriental art was one of his several avocations and late in his life he was in great demand as a lecturer on that subject.

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## VEGETATED CAYS

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Transformation of an unvegetated cay into a vegetated form depends to a large extent on stability, which in turn is a reflection of size and shape (Aston, 1995), availability of a source of water (a permanent water table is associated with cays with a minimum width of 300 m) and a source of viable seeds (via flotsam or from bird droppings). Large oval islands are the most stable with linear islands, often with highly mobile spits and large outcrops of beach rock, the least stable. Cemented deposits, especially beach rock, can form quickly and any erosion or movement of the island results in outcrops on the beach or even isolated on the reef flat. Also forming on cays on which significant numbers of birds nest is phosphatic cay sandstone formed by interaction of bird droppings or guano with the mineral substrate. Whilst beach rock is normally intertidal, the phosphate may be precipitated at the domed surface of the water table internally within the island, (Hopley, 1997; Hopley et al., 2007).

Even densely vegetated cays can be unstable and there are examples on the Great Barrier Reef (GBR) of vegetated cays disappearing completely (see Hopley et al., 2007). Changes can be brought about by storms or changing wind patterns (Flood, 1986), changes to sediment budgets or anthropogenic impacts. Erosion can expose mature soils and late successional stages of vegetation behind the beach, whilst the addition of new sediments will result in colonising vegetation being added at later stages.

Whilst colonising vegetation can be added to an unvegetated cay relatively quickly, the climax vegetation (e.g., *Pisonia* forest) with mature organic soils may take several 1,000 years to form. However, even in areas of the world where the relative sea level has been at or close to its present position for >6,000 years it is important to remember that mature coral cays were almost certainly non-existent during the Holocene transgression, significant for the birds and turtles which now use them as nesting sites. Vegetated cays also serve as roosting sites on bird migration routes and as sources of nutrients leached from guano and from rich organic soils, thereby enhancing algal growth on the reef flat (Chen and Krol, 1997). Vegetated coral cays are an integral part of reef-flat ecology but have a dubious future in the face of rising sea levels and modified sediment budgets produced by global climatic change.

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[Atoll Islands \(Motu\)](#)  
[Beach Rock](#)  
[Cay Formation](#)  
[Coral Cay Classification and Evolution](#)  
[Coral Cays-Geohydrology](#)  
[Coral Cays, Vegetational Succession](#)  
[Infrastructure and Reef Islands](#)  
[Phosphatic Cay Sandstone](#)  
[Soils of Low Elevation Coral Structures](#)  
[Unvegetated Cays](#)

## VOLCANIC DISTURBANCES AND CORAL REEFS

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## Definition

Volcanic eruptions refer to the release of volcanic ash and magma to the atmosphere and surrounding waters containing coral reefs.

## Introduction

Volcanoes have been emphasized in coral reef studies since Charles Darwin first formalized his thoughts surrounding the creation of tropical islands and atolls (Figure 1, Darwin, 1842). Volcanic activity is arguably the most influential natural disturbance that impacts reef growth and modern coral assemblages. However, its frequency of occurrence is much lower than other natural disturbances such as climate-induced bleaching and tropical cyclones. Physically, eruptions deliver hot magma that forms igneous rock of varying composition (Le Bas and Streckeisen, 1991), as well as volcanic ash, to the nearshore waters. Both can smother vast expanses of living coral reefs rapidly (Pandolfi et al., 2006), but longer-lasting, secondary impacts also exist. Volcanic ash particles contain numerous minerals in high concentrations that influence surrounding waters; most notably iron, magnesium, and silica (Flaathen and Gislason, 2007). Minerals from volcanic ash provide a pulse of key limiting ingredients that facilitate the rapid growth of phytoplankton, translating to enriched productivity of surface waters, often at the scale of entire oceanographic regions (Uematsu et al., 2004). These plankton blooms eventually die and decay, releasing nutrients and bacteria as they sink. Corals cannot uptake all of these available nutrients as fast as macroalgae, so following major volcanic ash input,



**Volcanic Disturbances and Coral Reefs, Figure 1** Anatahan, Commonwealth of the Northern Mariana Islands, following a 2003 eruption that provided no lava flow but lots of volcanic ash to surrounding waters.

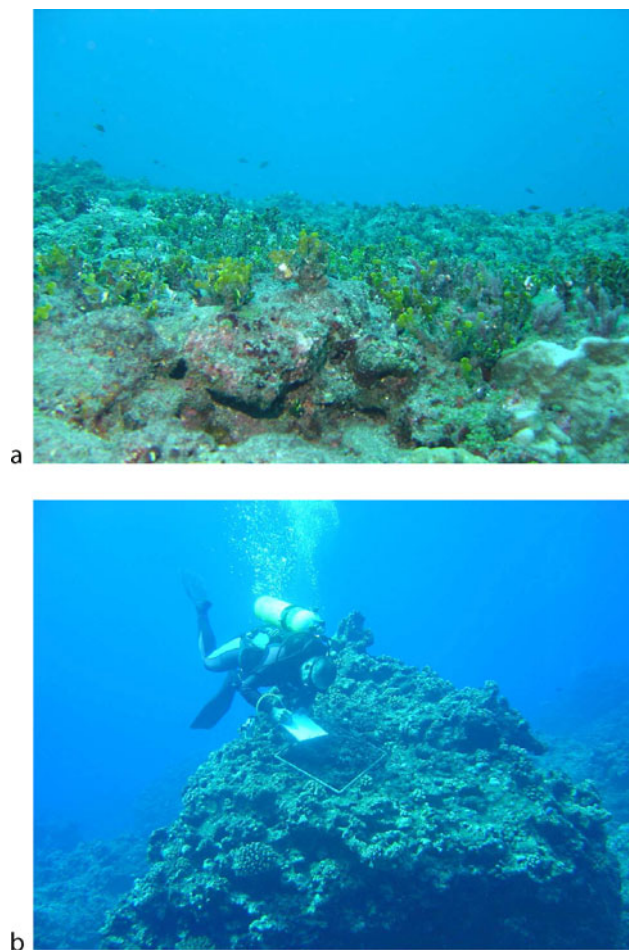
patches of macroalgae and cyanobacteria growth often emerge on the surrounding coral reefs. Even when the volcanic activity has ceased, re-suspension of volcanic ash during large-wave events can continue to facilitate this cycle, as well as increase turbidity levels and reduce the penetration of sunlight for substantial periods of time.

### Reef growth

It has long been recognized that igneous rock created from magma differs in porosity and permeability (Davis, 1969), and thus will provide for differential connectivity with island aquifer systems. Houk and Starmer (2010) show that the remote volcanic Mariana Islands, Western Pacific Ocean, have strikingly different (up to 1 part per thousand) ambient salinity levels, attributed to differential igneous rock porosity and permeability. In turn, this creates selective environmental conditions favorable for algae and sponge growth where low salinity exists, and increased coral growth where salinity is higher (Figure 2). The former yield low-rugosity reef structures with little three-dimensionality through time, while the latter provides for high-relief primary coral framework development. Clearly, volcanic bedrock is not all the same and differing characteristics have consequences for reef growth over time.

### Modern assemblages

Due to its rarity and unpredictable timing, relatively few studies have examined the impacts of volcanic activity upon reefs and subsequent recovery. Studies have shown that while lava flows are detrimental to living reef communities, regrowth of vibrant coral assemblages can occur within 5 years in Indonesia (Tomascik et al., 1996). In Hawaii, where wave exposure and seasonal temperature variation are much higher, studies suggest a much longer time period may be required for modern coral growth to return, up to 50 years (Grigg and Maragos, 1974). A 2003 eruption of Anatahan, Mariana Islands, yielded no lava flow but large quantities of volcanic ash that smothered most of the surrounding reef (Figure 1, Houk and Starmer, 2010).



**Volcanic Disturbances and Coral Reefs, Figure 2** Growth of modern assemblages on coral reefs surrounding volcanic islands strongly differs depending upon the characteristics of igneous rock. High-porosity bedrock has high connectivity with the islands aquifer and provides for continuous algae growth over time and low three-dimensionality of reef structure (a), compared with low-porosity systems (b).

Here, environmental conditions are similar to Hawaii and wind-generated waves often re-suspend volcanic ash, thus selecting against rapid coral settlement and growth. Predictions using other islands that have been erupting at varying times throughout the past 100 years revealed that ~90 years is estimated for coral abundance and species richness recovery to expected levels at the entire island scale.

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## Cross-references

[Antecedent Platforms](#)  
[Corals: Environmental Controls on Growth](#)  
[Darwin, Charles \(1809–1882\)](#)  
[Oceanic Hotspots](#)  
[Plate Tectonics](#)

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## VOLCANIC LOADING AND ISOSTASY

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The Earth's mechanical response to changes in surface loading is usually described in terms of local or regional isostasy in which the load is supported to varying degrees by the strength of the crust or lithosphere and by the reaction of the underlying mantle to the deformation of this layer.

For a general formulation for this response see Chapter *Glacio-Hydro Isostasy* and the response to volcanic loading can be seen as a special case of this. The essential differences between the two cases are (1) the timescale of loading is usually much longer than that of the glacial cycles, (2) the length scale of the loads are shorter than that of the large ice sheets, (3) the load-stress magnitude of the volcanic load may be much larger than that of ice loads and (4) the volumes of the volcanic loads are comparatively small such that when the volcanoes form in an ocean environment the water displaced and the concomitant hydro-isostasy can usually be ignored.

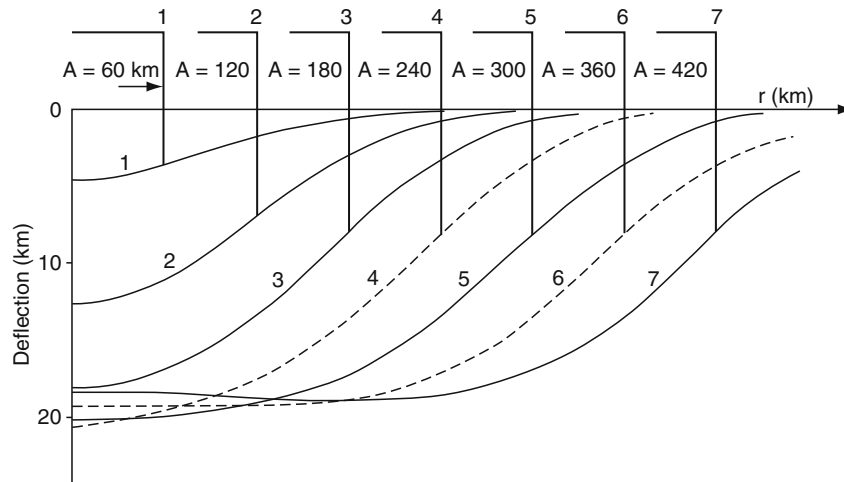
The formation of large volcanic complexes usually occurs over periods of a million years or longer. This is greater than the typical relaxation time of the mantle inferred from the glacio-hydro isostatic analyses such that the mantle can usually be considered as a fluid of zero viscosity. However, the loading time is likely to be comparable to the relaxation times of the lithosphere, particularly for the lower lithosphere, such that the viscosity structure of the lithosphere may be important. The smaller length scale of the volcanic loads and the unimportance of the hydro-isostatic loading means that the isostatic models need not be global and flat-earth representations are usually adequate. But, combined with the load-stress magnitudes being generally larger, it also means that the structure of the crust and the lithospheric part of the mantle may also be important in determining the isostatic response. The larger load stresses also mean that elastic failure of the crust may occur. Another difference between the two loading problems is that the process of volcanic loading itself may have a modifying effect on lithospheric properties because of heat transport into the lithosphere during the active phase of loading.

The isostatic response to volcanic (and sediment) loads can be qualitatively represented by the regional isostatic model in which the stress-bearing layer overlies a fluid mantle of zero viscosity. Usually, this layer will have depth-dependent physical properties but for computational convenience any lateral variability is usually ignored. The time history of loading is also mostly ignored. [Figure 1](#) illustrates the schematic elastic response for a disk-shaped load for which there exist convenient analytical solutions (such solutions also exist for other axially symmetries such as parabolic profile loads). The deformation beneath the load is characterized by a “flexural parameter” or “radius of relative stiffness,”  $l$ , defined as

$$l^4 = D/(\rho_m - \rho_l)g$$

$D$  is the flexural rigidity and for a depth ( $z$ ) dependence of elastic parameters (shear modulus  $\mu$  and bulk modulus  $K$  with  $\lambda = K - (2\mu/3)$ ) where the integration is across the elastic layer from its upper surface  $z = +H/2$  to its lower surface  $z = -H/2$ . For typical elastic parameter values,  $l \approx 50$  km and much of the spatial variation in the deformation occurs over a distance of about  $4l$ .





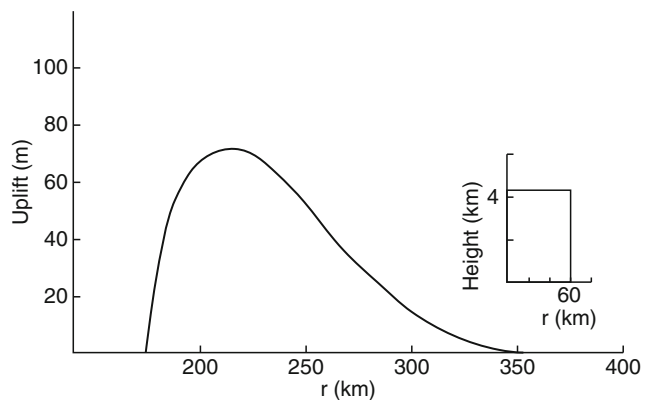
**Volcanic Loading and Isostasy, Figure 1** Deflection of an elastic plate of flexural rigidity  $D$  overlying a zero viscosity fluid, subject to a disk load of variable radius  $A$ , density  $2.8 \text{ gm/cm}^3$  and height  $5 \text{ km}$ . The moat forming at the edge of the load is assumed to be filled in with material of the same density up to the level of the undeformed surface consistent with the definition of  $D$  used here. From Lambeck and Nakiboglu (1980).

Once the load radius exceeds about  $3-4l$ , the displacement beneath the center of the load approaches that of local isostatic compensation (see Chapter *Glacio-Hydro Isostasy*) with a maximum displacement of  $z_{\text{max}} \approx -(\rho_l/\rho_m)h$  where  $h$  and  $\rho_l$  are the height and density of the load ( $h$  is measured with respect to the undeformed surface). Solutions (1, 2) in Figure 1, with a load radius of up to about  $100 \text{ km}$ , are representative of single volcanic complexes, whereas the larger diameter loads are more representative of basaltic plateau or large sedimentary loads. The solutions for large radius begin to resemble the surface deflection across continental margins from melt-water loading in the glacio-hydro isostatic problem.

Normally, a broad trough develops around the load down to a maximum depth of  $z \approx 0.5z_{\text{max}}$  that can be expected to be partly filled as part of the volcanic complex and partly by water if the formation is in an ocean environment. This is seen around some of the large volcanic complexes such as the Hawaiian chain. Thus, in more realistic models the question of how this moat is filled must be considered. Beyond the moat, a small uplifted bulge occurs on the order of some tens of meters in peak amplitude and typically  $100-150 \text{ km}$  in width (Figure 2), with the actual dimensions being a function of the lithospheric parameters, load dimensions and the degree to which the moat has been filled.

If a viscous component is introduced to describe stress relaxation in the lithosphere, particularly in the lower part of this layer, then the sea floor subsides until the local isostatic limit is approached and the outer bulge migrates inwards.

Observational evidence that supports these models of regional compensation or lithospheric flexure comes from gravity (including geoid), seismology and sea-level



**Volcanic Loading and Isostasy, Figure 2** Uplift of the peripheral bulge for the disk load of  $60 \text{ km}$  radius. From Lambeck (1981).

investigations. The seismological evidence includes mapping of the slope of seismic reflectors within the crust beneath the load and moat and variations in the depth of the Moho. The seismic data can also define some of the internal crustal structure beneath the volcano and establish whether faulting has occurred as a result of loading. Gravimetric and geoid surveys indicate positive anomalies over seamounts and volcanoes that are consistent with the mass distribution within the regional compensation models and permit the flexural parameters to be estimated. Primary outcome of such studies include estimates of the effective elastic thickness of the lithosphere, the dependence of  $D$  on the age of the lithosphere at the time of volcanic seamount formation, and evidence for relaxation of the load stress for the larger volcanic

loads. These estimates of the effective elastic thickness are generally significantly less than the estimates from hydro-isostatic analyses, indicating that stress relaxation occurs in the lower lithosphere on timescales between the glacial cycles and volcanic loading and longer. The sea-level data point to the uplift of atolls and other islands positioned on the peripheral bulge. This appears, for example, to have been the case for Henderson Island that was uplifted as a result of the formation of the Pitcairn volcanic complex at  $\sim 0.8$  million years ago. Another example is the island of Makatea which was probably uplifted during the formation of the Tahiti volcanic complex.

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## Cross-references

[Glacio-Hydro Isostasy](#)

# W

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## WACKESTONE

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Wackestone is a type of limestone recognized in the Dunham (1962) Classification Scheme in which grains make up more than 10% of the rock but the grains are mud supported, i.e., the grains float in a mud matrix.

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### Cross-references

[Porosity Variability In Limestone Sequences](#)

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## WALTHER, JOHANNES (1860–1937)

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Germany

Johannes Walther was one of the founders of sedimentology and paleoecology (Middleton, 1973; Seibold, 1992; Ginsburg et al., 1994), and conducted four fundamental studies on modern coral reefs (Walther, 1885, 1888, 1891, 1910). Walther was born on 20 July 1860 in Thuringia, Germany. He studied geology and biology at the University of Jena, where his mentor was the famous biologist Ernst Haeckel. Walther completed his Ph.D. in 1886. Subsequently, he studied modern algal reefs in the

Mediterranean and fossil reefs in the Tertiary of Sicily and in the Triassic of the Austrian Calcareous Alps (Walther, 1885). He was among the first who recognized the significance of calcareous algae as reef builders. Based on his studies in the modern reefs, and using thin-section and chemical analyses, he attempted to explain the textures he found in the fossil reef limestones. In his work on the coral reefs of the Sinai Peninsula, Walther (1888) was able to study modern and elevated subfossil reefs nearby. The latter offered three-dimensional sections, which led Walther to the conclusions that only 40% of a reef is formed by coral framework and that 60% is made of detritus filling the interstices. Furthermore, he realized the importance of antecedent topography for reef development and distribution. Walther (1891) established his findings when studying modern and subfossil reefs between India and Ceylon. Again, he stressed the importance of detritus in reefs and the fact that a great part of this material is produced by the destructive activity of organisms. Also, he considered changes in relative sea-level, when discussing subfossil reef terraces. In 1890, Walther became a Professor at the University in Jena. From 1906 to 1928, he held the chair of geology and paleontology at the University of Halle. He returned to the algal reefs in the Mediterranean in 1910 and found significant facies changes that had occurred over the past 25 years, geologically a very short time period. In 1914, Walther was able to visit the Great Barrier Reef of Australia, but he had to return home early due to the outbreak of WW I. Unlike other reef researchers during that time period, Walther did not contribute to the coral reef problem, i.e., the interpretation of shallow atolls and barrier reefs in oceanic settings in the light of Darwin's (1842) subsidence theory. Even so, he was among the first to recognize the importance of calcareous algae for reef-building, described what is today called bioerosion, in great detail, hinted to the significance of loose sediment



in modern reefs, and elaborated the meaning of antecedent topography for reef development. Walther died on 4 May 1937 in Hofgastein, Austria.

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## Cross-references

[Antecedent Platforms](#)  
[Binding Organisms](#)  
[Bioerosion](#)  
[Fringing Reefs](#)  
[Darwin, Charles \(1809–1882\)](#)  
[Holocene Reefs: Thickness and Characteristics](#)  
[Red Sea And Gulf Of Aqaba](#)  
[Rhodoliths](#)

## WAVE SET-UP

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### Definitions

**Wave run-up.** The vertical distance between the ocean (tide) level and the maximum height reached by the uprush of waves breaking on a beach or structure.

**Wave set-up and set-down:** Positive and negative changes in mean water level produced as waves shoal and break on beaches and reefs.

**Wave thrust:** A vertically integrated force per unit wave crest length produced by changes in wave momentum as waves propagate in shoaling and shallow water. It has two components; an isotropic pressure and a unidirectional force in the direction of wave propagation. Also known as radiation stress.

**Shoaling.** The process by which the wave height, length, celerity and other properties of the waves change as they travel from deep(er) water into shallow(er) water.

See also Chapter [Waves and Wave-Driven Currents](#) for definitions of other terms concerning waves.

Mathematical symbols are defined where they first appear in the text, or on a relevant figure. The subscript *o* refers to the deep water values of the various quantities.

### Introduction

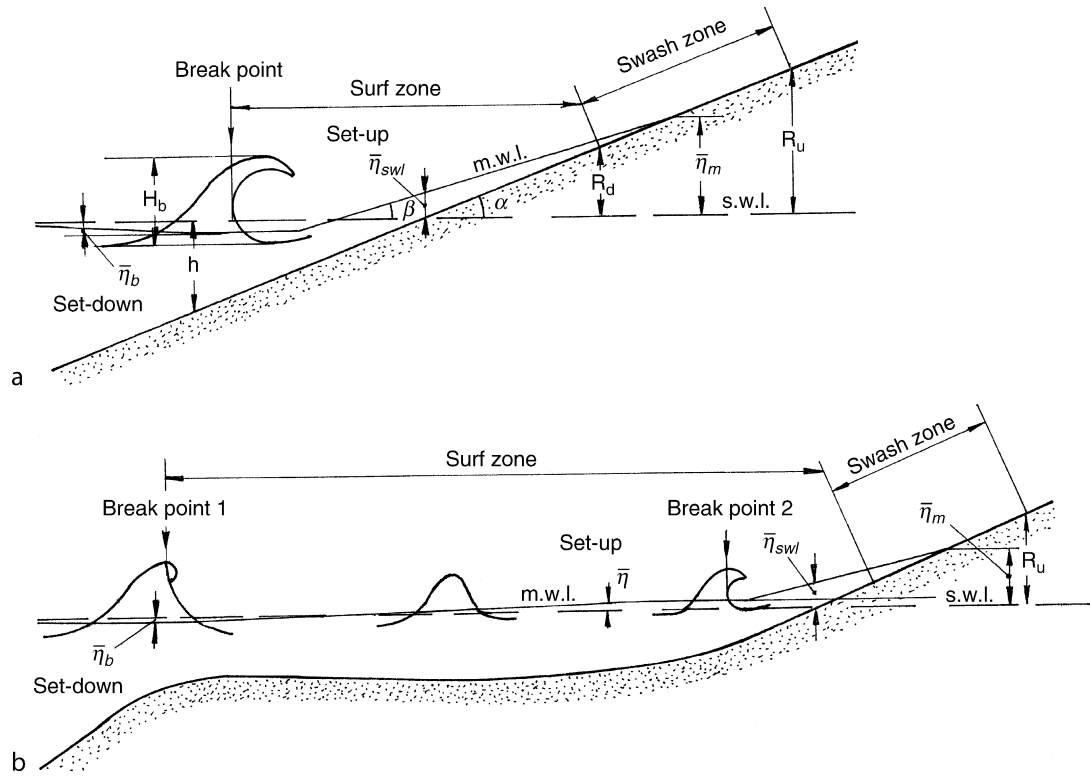
In the late 1940s, it was observed at Bikini Atoll that the predominant 12–15 s swell waves breaking on the reef caused a significant inflow of ocean water into the atoll lagoon. The accompanying increase in water level in the lagoon, known as wave set-up, was 0.45–0.6 m (Munk and Sargent, 1954; Von Arx, 1954). As the significance of waves as a dominating agent in determining reef-top morphology and ecology was increasingly recognized in the late 1970s and the 1980s, it became apparent that wave set-up plays a significant role in defining wave-driven current systems on coral reefs (e.g., Roberts, 1981; Hearn et al., 1986). (see Chapter [Waves and Wave-Driven Currents](#)).

Wave set-up is also an important factor, particularly in microtidal environments, in determining groundwater levels in beaches on coral cays or other reef-protected shorelines. These wave-induced groundwater levels influence the formation of *Beach Rock*, as well as the success of turtle nesting behind the beach. Wave set-up and associated wave run-up also have been identified as important factors in causing flooding of low-lying reef-protected coasts and reef islands (see Chapter [Infrastructure and Reef Islands](#)).

### Wave set-up on beaches

A wave train propagating onto a beach or reef produces changes in mean pressure within the water and a unidirectional force in the direction of wave propagation (Longuet-Higgins and Stewart, 1964). This wave thrust increases as the water depth decreases. On a beach offshore of the breaker zone, if it is assumed that there is no frictional dissipation at the bottom, the increasing wave thrust is balanced by a change in mean hydrostatic pressure such that the mean water level decreases as the waves propagate shoreward, that is, wave set-down occurs. Within the surf zone where energy is being dissipated by wave breaking, the wave thrust decreases as the breaking surge travels shoreward and consequently the mean water level rises, that is, wave set-up occurs ([Figure 1a](#)).

[Figure 1a](#) shows the occurrence of wave set-down and set-up on a relatively steep beach. The still water level (s.w.l.) is the water level if there were no waves present and is the reference level for measuring set-down and set-up. In an oceanic situation the s.w.l. will vary with the tides and meteorological influences such as storm surge. The changes in mean water level (m.w.l.) occur when waves approach, shoal, break and run up the beach. The m.w.l. can not be seen but it can be measured either as the time-averaged mean position of the water level at any specific location approaching and within the surf zone or



**Wave Set-Up, Figure 1** Wave set-up on beaches. (a) Waves breaking on a steep, plane beach. (b) Waves breaking on a beach with offshore bar.

as the mean hydrostatic pressure on the bottom at that location. Maximum set-down  $\bar{\eta}_b$  occurs in the vicinity of the break point; the maximum set-up  $\bar{\eta}_m$  occurs where the m.w.l. intersects the beach face. However, measurements of set-up in the swash zone are not always reliable and there are differences of opinion as to their meaning (Gourlay, 1992). Some researchers prefer to refer to the set-up measured at the location where the s.w.l. intersects the beach profile (Dean and Walton, 2009).

If it is assumed that the height of the breaking surge is a constant fraction  $\gamma$  of the actual water depth  $d$  (including set-up  $\bar{\eta}$ , i.e.,  $d = \bar{\eta} + h$ ) in the surf zone, the theory of Bowen et al. (1968) predicts that the ratio of the m.w.l. slope in the surf zone  $\tan \beta$  to the beach slope  $\tan \alpha$  is a simple function of  $\gamma$ , that is,

$$\tan \beta / \tan \alpha = K = 1 / \left( 1 + \frac{8}{3\gamma^2} \right)$$

Laboratory experiments (Bowen et al., 1968) confirmed the existence of set-down and set-up on plane beaches. Subsequent analysis of a wide range of laboratory data for impermeable plane beaches suggested that the maximum set-up on fairly steep beaches ( $\tan \alpha \leq 0.1$ ) is about 30% of the initial breaker height  $H_b$ , whereas for flat beaches ( $\tan \alpha \leq 0.04$ ) it is only 15% of it (Gourlay, 1992). For comparison, wave set-down probably would be no more than 5% of the breaker height.

Nielsen (1988) measured wave set-up on a beach at Dee Why, NSW, which has a relatively steep face and an offshore bar. There were different set-up profiles for small and large waves. Small waves broke directly on the beach face creating a steep m.w.l. gradient shoreward of the initial breakpoint. Large waves broke on the offshore bar or flatter portions of the profile. In this case, the m.w.l. had two distinct gradients, a flat one in the outer surf zone and a steeper one following a second break point inshore on the beach face (Figure 1b). These experiments also revealed that, even if there were no rainfall, the groundwater level behind the beach is elevated above the ocean tide level. This groundwater level varies with changes both in the height of the waves and in tide levels. Laboratory experiments on wave-formed beaches (Gourlay, 1992) indicated wave set-up profiles for large and small waves similar in general form to those observed by Nielsen. They also showed that, for steep beaches, the wave set-up and hence the wave-induced groundwater level were larger for beaches formed of fine sand in comparison with those formed of medium sand or fine pebbles (see discussion below). Recent analyses of various field data indicate that the set-up at the still water line is about 20% of the significant wave height  $H_{os}$  with a variation of about  $\pm 10\%$  (Dean and Walton, 2009).

Set-up  $\bar{\eta}_m$  should not be confused with run-up  $R_u$ . The latter term refers to the maximum vertical height on the beach reached by the swash/uprush from the breaking

waves. Run-up is commonly measured relative to s.w.l. on beaches and engineering structures but this may not be appropriate for reef-protected beaches (see discussion below). For a plane beach or structure, the run-up is related to the wave conditions and beach slope by the following equation:

$$\frac{R_u}{T\sqrt{gH}} = C \tan \alpha$$

where the parameter  $C$  ( $\leq 1$ ) varies with the roughness and permeability of the beach (see Nielsen, 2009).

### Wave set-up on coral reefs

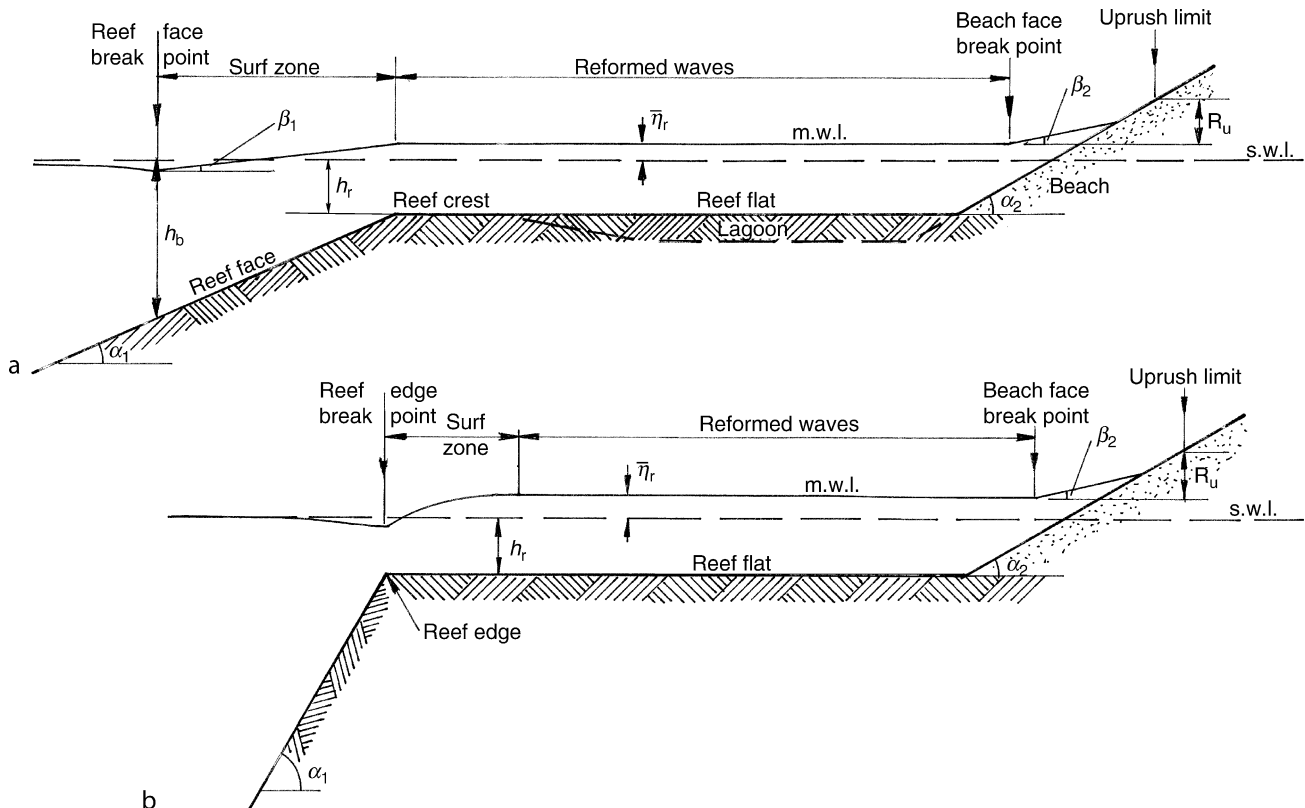
Wave set-up on reefs is governed by the same theoretical principles as wave set-up on beaches. However, there are some differences in approach because the morphology of reefs is different from that of beaches. In general, the profile of a reef will have a reef face of variable slope, a reef crest/rim, and a reef flat and/or lagoon. In the case of a fringing reef or cay on a platform reef, normally there will be a relatively steep beach at the far side of the reef flat (Figure 2). With a platform reef or atoll lagoon, there will be a leeward reef rim or reef.

When the reef face is not too steep ( $\tan \alpha < 0.1$ ) and the waves break on it, the theory of Bowen et al. (1968) for set-up on a plane beach has been applied by Tait (1972)

to give an estimate of wave set-up on a horizontal reef top. As reef faces are generally much rougher than sandy beach profiles, bottom friction may be significant and probably will reduce the wave height and hence the wave thrust sufficiently to eliminate any wave set-down on the reef face prior to breaking. With this assumption, the wave set-up  $\bar{\eta}_r$  on a horizontal reef is given by  $\bar{\eta}_r = K(h_b - h_r)$  (Figure 2a). The set-up is maximum when  $h_r = 0$ , i.e., when the tide level is equal to the reef top level, and it reduces to zero when  $h_r \geq h_b$ , i.e., when waves pass over the reef without breaking.

During the period between 1980 and 1996, several researchers measured wave set-up on laboratory models of coral reefs with widely varying profiles (Gourlay, 1996a,b). Reef-face slopes varied from greater than 1 in 50 to vertical. One model reproduced a platform reef with flow across it, whereas all the others were fringing reefs with horizontal or very flat reef tops; one of these latter had a shallow lagoon between the reef crest and the beach behind the reef. Two models involved experiments with irregular waves as well as regular ones. In only one case was any attempt made to measure the wave set-up on the actual reef in the field.

In general, these laboratory experiments indicate that wave set-up on a quasi horizontal reef increases with both increasing ocean wave height and wave period and decreasing water depth over the reef top. No wave set-up



Wave Set-Up, Figure 2 Wave set-up on coral reefs. (a) Waves breaking on reef face. (b) Waves breaking at reef edge.



occurs if the water depth is large enough for the waves to pass over the reef without breaking. This situation occurs when the deep water ocean wave height  $H_o$  is less than  $0.4 h_r$ . For steep-faced reefs, waves which just pass over the reef edge may break on the reef top, whereas larger waves will break at the reef edge.

For waves breaking on the top of a steep-faced reef (Figure 2b), a theoretical analysis using wave thrust theory predicted that the set-up on a horizontal reef is about 14% of the ocean wave height (Gourlay, 1996a). This is close to the maximum set-up on a flat beach.

For flatter reef faces (Figure 2a), larger waves break on the reef face seaward of the reef crest and in some cases dissipate significant energy before the broken waves reach the reef crest. In these latter situations, wave set-up on the reef top approaches a limiting value with increasing wave height. Furthermore, the magnitude of the set-up on the reef top decreases as the slope of the reef face decreases. Analysis of experimental data for both steep and flatter reef faces shows that wave set-up on the reef top increases with increasing  $H_o^2 T$ , which quantity is proportional to the ocean wave power or energy flux (Gourlay, 1996b) (see Chapter *Waves and Wave-Driven Currents*).

Munk and Sargent (1954) first suggested a possible relationship between wave set-up on coral reefs and ocean wave power. Gourlay (1996b) applied this principle to waves breaking at the edge of a steep-faced horizontal reef. This analysis produced a relationship for wave set-up on a steep-faced horizontal reef which reduces to the following form:

$$\bar{\eta}_r = \frac{0.015 K_p g^{1/2} H_o^2 T}{d_r^{3/2}} \left[ 1 - 0.16 \left( \frac{d_r}{H_o} \right)^2 \right]$$

where the reef profile factor  $K_p$  ( $\leq 1$ ) varies with the reef face slope  $\tan \alpha$  and  $d_r$  is the water depth, including wave set-up, on the reef top. Ocean waves are variable in height and period and are commonly represented by the significant wave height  $H_{os}$ . In calculating wave set-up on a reef,  $H_o$  in the above formula is the height of a regular sinusoidal wave, which is equivalent to the root-mean-square wave height  $H_{orms}$  ( $= \frac{H_{os}}{\sqrt{2}}$ ) of irregular ocean waves (see Chapter *Waves and Wave-Driven Currents*).

Numerical models which reproduce wave transformation and breaking on flatter but still relatively steep reef faces have been developed by other researchers. Both Skotner and Apelt (1999) and Massel and Gourlay (2000) have computed wave set-up values which agree reasonably well with those measured on laboratory models with different reef face slopes and profiles.

Irregular ocean waves tend to occur in groups of larger waves followed by groups of smaller waves. These groups of larger waves pump water onto the reef top or lagoon, increasing the set-up above its mean value but the following groups of smaller waves are unable to sustain this higher water level and water flows back seawards over the reef rim reducing the set-up below the mean value.

Hence, the wave groups create a dynamic component of wave set-up which is superimposed upon the steady wave set-up calculated using  $H_{orms}$ .

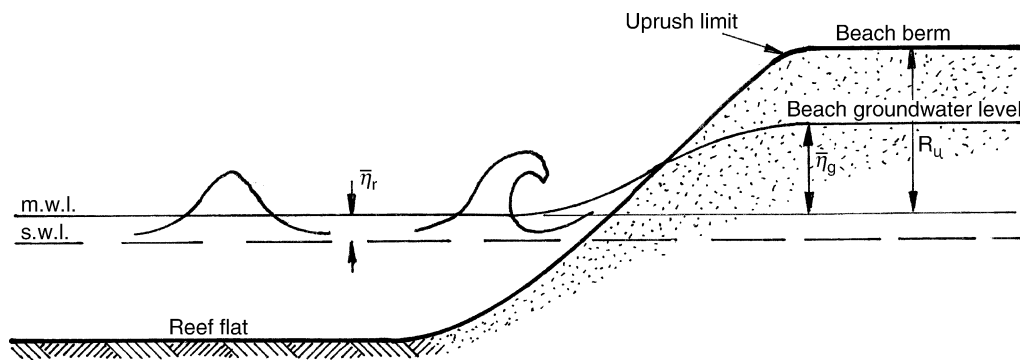
The magnitude of the dynamic set-up or surf beat depends upon the width of the reef. The wider the reef the greater its capacity to absorb and smooth out the fluctuations in set-up resulting from the wave groups. On the other hand, the dynamic set-up fluctuations decrease in magnitude as the water depth over the reef crest decreases, even though the magnitude of the steady wave set-up increases with decreasing water depth. Hence, surf beat will be more significant at high tide than low tide and at high spring tides than neap tides (Seelig, 1983; Gourlay, 1996b).

In certain situations, resonant surf beat oscillations may be instigated by the coincidence of the wave group period with the natural period of oscillation of the water body on the reef flat. Substantial amplification of the surf beat at the shoreline and consequent severe erosion or damage to shore facilities is possible (Nakasa and Hino, 1990).

Recent laboratory and numerical modeling studies on the same reef profile as used in Seelig's experiments show clearly the influence of surf beat (infragravity waves) in producing resonant set-up oscillations on a narrow coral reef. Such oscillations dominate the run-up on a reef-protected beach (Nwogu and Demirbilek, 2009). Field observations following Typhoon Rus at Guam in 1991 found an inverse relationship between reef flat width and overwash height (run-up). That is, the highest overwash occurred along steep coasts adjacent to narrow reef flats where the contribution of waves to overwash was greatest (Jaffe and Richmond, 1993).

Various theoretical and empirical formulae representing the processes just described have been utilized for calculating estimates of the wave set-up on a coral reef and the conditions under which a reef-top island is likely to be flooded during an extreme event (Gourlay, 1996b; 1997). After an allowance has been made for storm surge, these calculations initially determine the set-up resulting from waves breaking on the reef rim and then consider the influence of the surf beat upon water levels in the lagoon. Calculation of the wave run-up on the beach, relative to the m. w. l. on the reef top, gives another estimate of the waves' flooding potential for a specific situation. Such calculations clearly show both the protective action of coral reefs in reducing the size of waves breaking on reef island beaches and the potential for wave set-up to raise reef-top water levels significantly higher than high tide level and hence flood reef islands during extreme events.

To determine the wave-induced groundwater level  $\bar{\eta}_g$  behind the beach (Figure 3), it is necessary to calculate the wave set-up caused by the residual waves breaking on the relatively steep plane reef island beach for the appropriate ocean tide plus set-up water level on the reef top in front of the beach. At the time of writing, there is no simple way for calculating the wave set-up in a permeable beach of a particular sand size, let alone for a permeable beach comprised of a wide range of materials, such as is frequently found on reef island beaches. However, advanced numerical modelling simulating the



**Wave Set-Up, Figure 3** Wave set-up, wave run-up and wave-induced groundwater for a reef top beach.

interaction between waves and beach groundwater has produced encouraging results when compared with experimental laboratory data for a beach of a homogeneous sand (Ang et al., 2004). The ground water level behind a reef island beach will also be affected by changing tide levels on the reef flat, as well as rainfall on the island.

### Measurements of wave set-up on coral reefs

There have been very few actual measurements of wave set-up on coral reefs. Apart from situations where set-up caused by swells from distant storms or hurricanes has resulted in flooding or damage to infrastructure on reef islands (Gourlay, 1996b; Amanaki et al., 2003), the most complete set of field data of wave set-up across a reef flat has been obtained by Jago et al. (2006) at Lady Elliot Island, the southernmost reef in the Great Barrier Reef region. These measurements were made with simple slow response stilling wells and measuring techniques similar to those developed by Nielsen (1999) for measuring wave set-up on beaches. Waves and mean water levels were measured over both rising and falling tides during low to moderate wave conditions ( $H_{os} < 0.5$  m). Both wind waves and swell were present. The spring and neap tidal ranges at this site are 1.7 m and 0.9 m, respectively. The set-up was observed to vary both spatially and temporally across the reef with changing water depth. At low tide, both wind waves and swell broke on the reef edge generating set-up on the reef flat. At midtide, set-up occurred both at the reef edge, where wind waves broke, and on the island's beach, where the swell broke. At high tide, no waves broke at the reef edge and there was negligible set-up there but significant set-up occurred on the beach, where both wind waves and swell broke. Set-down also was observed both on the reef face before waves broke on the reef edge and on the reef flat as waves passed over the reef rim into deeper water on the reef flat.

Recent measurements of wave set-up and wave-driven currents in an atoll lagoon in the Cook Islands have shown that wave pumping drives the flushing of these lagoons

when there are no deep passages or gaps in their surrounding reef (see Chapter *Waves and Wave-Driven Currents*).

### Summary

Waves breaking on a reef or beach create an increase in m.w.l. in the surf zone called wave set-up. This set-up increases with increasing height and period of the ocean waves and decreases with increasing water depth over the reef, becoming negligible when waves pass over the reef without breaking. Maximum set-up occurs when the ocean water (tide) level is about the same level as the reef top. The water level differences caused by wave set-up drive reef-top current systems and the flushing on many atoll lagoons. Wave set-up may contribute significantly to the groundwater elevation in cays and the sedimentary margins of continental islands. Wave set-up caused by both local storm waves and swells from distant storms may cause significant flooding, erosion and damage on reef islands, particularly where resonant oscillations occur on a reef top.

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## Cross-references

[Cay Formation](#)  
[Fringing Reef Circulation](#)  
[Hydrodynamics of Coral Reef Systems](#)  
[Infrastructure and Reef Islands](#)  
[Lagoons](#)  
[Reef Front Wave Energy](#)  
[Waves and Wave-Driven Currents](#)  
[Wave Shoaling and Refraction](#)

## WAVE SHOALING AND REFRACTION

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### Definitions

**Diffraction.** The process by which wave energy is transmitted laterally along a wave crest into a sheltered zone. Most commonly observed behind breakwaters, small islands and exposed reefs which create a sheltered zone behind them.

**Orthogonal.** A line at right angles to the wave crest indicating the direction of travel of the wave. Also known as wave ray.

**Refraction.** (1) The process by which the direction of a wave moving in shallow water at an angle to the bottom contours is changed; the part of the wave crest advancing in shallower water moves more slowly than the part of the crest still advancing in deeper water. (2) The bending of wave crests by currents.

**Shoaling.** The process by which the wave height, length, celerity and other properties of the waves change as they travel from deep(er) water to shallow(er) water.

See also *Waves and Wave-Driven Currents* for definitions of other terms concerning waves.

Mathematical symbols are defined where they first appear in the text, or in a relevant figure. The subscript *o* refers to the deep water values of the various quantities.

### Introduction

When ocean waves propagate around or onto coral reefs, their characteristics change as they interact with the changing seabed morphology. The resulting changes in wave height and direction determine when and where waves break and the patterns of wave crests and wave-driven currents that develop on a given reef.

### Shoaling of waves

The shoaling process occurs as waves approach a straight beach or reef face with their crests parallel to the bottom contours. As waves propagate from deep water into water of decreasing depth *h*, both their celerity *C* and length *L* decrease (see *Waves and Wave-Driven Currents*). The wave height *H* also changes, eventually becoming increasingly larger until the waves break.

In the simple case of swell propagating from deep water into shallow water with no reflection and no dissipation of wave energy, energy conservation requires that the wave power remains constant (see *Waves and Wave-Driven Currents*). Using these assumptions with small amplitude (sinusoidal) wave theory gives the following relationship for the variation of wave height as a wave train propagates shoreward toward a beach or over a gently sloping reef face.

$$\frac{H}{H_o} = \frac{C_o}{2nC} = K_s$$



where  $K_s$  is the shoaling coefficient and  $n = C_g/C$ , where  $C_g$  is the group velocity. The parameter  $n$  varies with the relative depth  $h/L$  or  $h/L_0$ .

In shallow water, where  $C = \sqrt{gh}$ ,

$$K_s = \left( \frac{8\pi h}{L_0} \right)^{-\frac{1}{4}}$$

Finite amplitude (cnoidal) wave theory indicates that the shoaling in reality is accentuated as the ocean wave steepness  $H_0/L_0$  increases and is much more pronounced than predicted by small amplitude theory (Figure 1). Hence, the latter does not adequately predict wave heights prior to the occurrence of wave breaking, which will occur in shallow water when  $H/h$  approaches 0.8.

### Refraction of waves

In shoaling water when the wave crests cross the depth contours at an angle  $\theta$ , that part of the wave crest which first reaches a given water depth is slowed down relative to the rest of the crest and the wave crest becomes curved. The wave direction is changed and the crests tend to become parallel with the depth contours (Figure 2). For example, when long-crested waves of constant period cross a simple straight step from depth  $h_1$  into shallower depth  $h_2$  (Figure 3) simple geometry leads to the result  $\sin \theta_2 / \sin \theta_1 = C_2 / C_1$  or  $\sin \theta / C$  is a constant. This is the well-known Snell's Law, which also governs the refraction of light at the boundary between two materials with different refractive indices.

Refraction not only causes the wave crests to bend as the wave direction changes but the spacing  $b$  between the orthogonals also changes (Figure 2). When waves approach a straight plane beach at an angle, the spacing between orthogonals increases and hence the wave height reduces. Assuming that the wave energy between orthogonals remains constant, this change in wave height is

given by the refraction coefficient  $K_R = \sqrt{(b_0/b)}$  and is additional to that caused by shoaling. Hence, the wave height in shallow water is given by  $H/H_0 = K_R K_s$ .

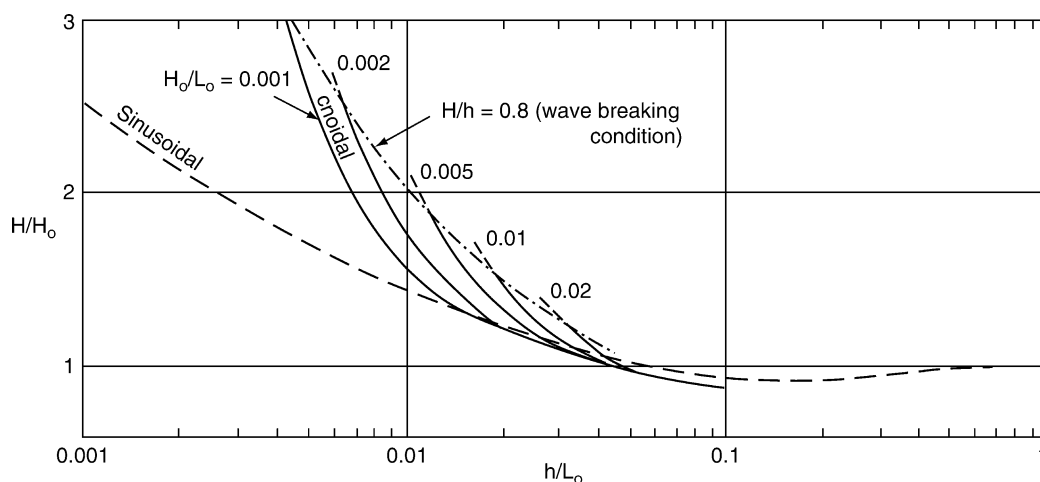
Refraction thus results in an additional change in wave height over and above that which occurs due to the direct shoaling effect. In general, a decrease in spacing of the orthogonals represents an increase in wave height while an increase in orthogonal spacing represents a decrease in wave height. This results in wave energy being either concentrated behind submarine ridges and on headlands or dispersed behind submarine canyons and in bays. Submerged shoals and reefs usually focus wave energy behind them (Figure 4).

Where orthogonals intersect, as in Figure 4b, the simple theory breaks down. Two new processes come into play. Firstly, when there is a large change of wave height along a short length of wave crest, energy will be transferred laterally along the crest by the process known as diffraction which will tend to reduce the concentrating effect of refraction. Furthermore, as the concentrated waves travel into increasingly shallow water they will deform and eventually break, dissipating a significant amount of their energy. Where waves break at an angle to the shoreline, alongshore currents will be generated (see *Waves and Wave-Driven Currents*).

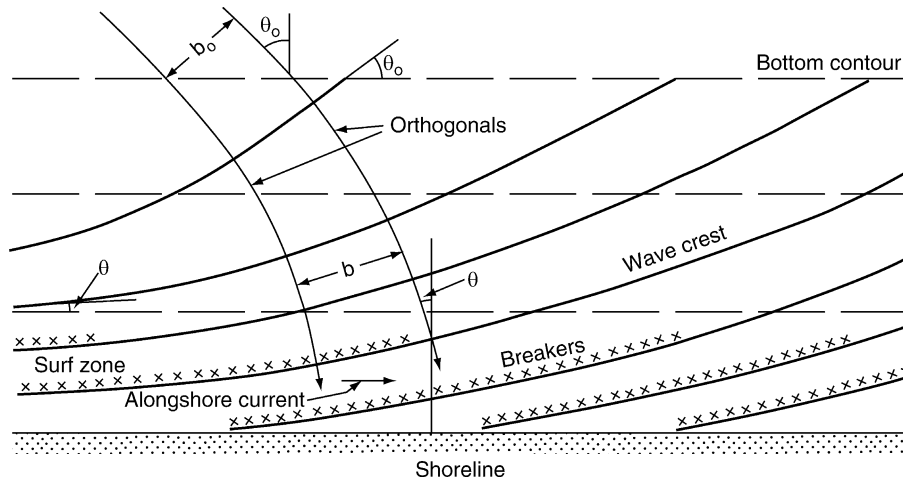
Formerly, wave refraction diagrams, showing the effect of natural bottom topography in changing wave directions and heights within a particular area, were produced manually using graphical procedures. These diagrams are now produced with digital computers using numerical modeling techniques, based upon the differential equation relating the bending of an orthogonal to the change in wave celerity (see Dean and Dalrymple, 1991).

### Refraction of waves by currents

The previous discussion of wave refraction assumes that the only movement of the water is that caused by the



**Wave Shoaling and Refraction, Figure 1** Comparison between shoaling coefficients according to small amplitude (sinusoidal) and finite amplitude (cnoidal) wave theories (from Svendsen and Brink-Kjaer, 1973).



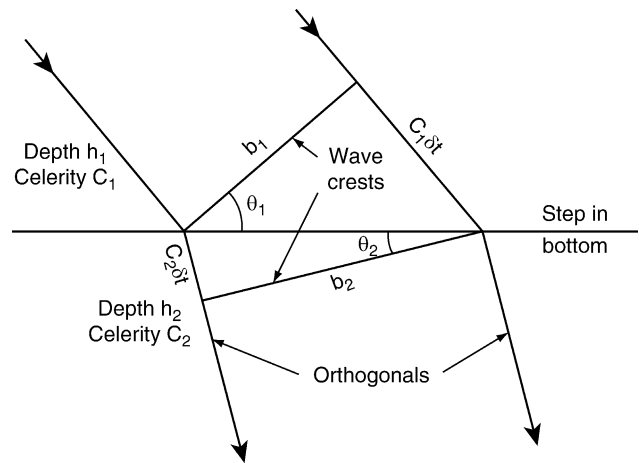
**Wave Shoaling and Refraction, Figure 2** Wave refraction when waves approach a plane beach travelling from deep water into shallow water.

waves and that refraction is caused by changes in wave celerity as waves cross the bottom contours at an angle. However, if there are tidal currents, wind- or wave-driven currents or flow from a river mouth or a stormwater outlet, then the waves will be affected by those currents. If the waves are travelling in the same direction as the current, then their celerity will increase and they will become longer and flatter. If the waves are travelling in the direction opposite to the current, their celerity will decrease and they will become shorter and steeper and breaking may occur earlier than when no current is present. If waves cross a region where the current velocity varies in the horizontal plane, refraction will occur as the wave crests bend under the influence of the different current velocities (Nielsen, 2009).

### Wave refraction around reefs

Wave refraction around small platform reefs is an essential process in the formation of many reef-top islands. In the simplified examples shown (Figure 5), deep water ocean waves are refracted at the vertical reef face where the wave direction changes abruptly in accordance with Snell's law. They then propagate on the reef top as shallow water waves. If the waves are large enough to break on the reef rim, they will generate an alongshore current flowing along the reef rim toward the leeward end of the reef platform.

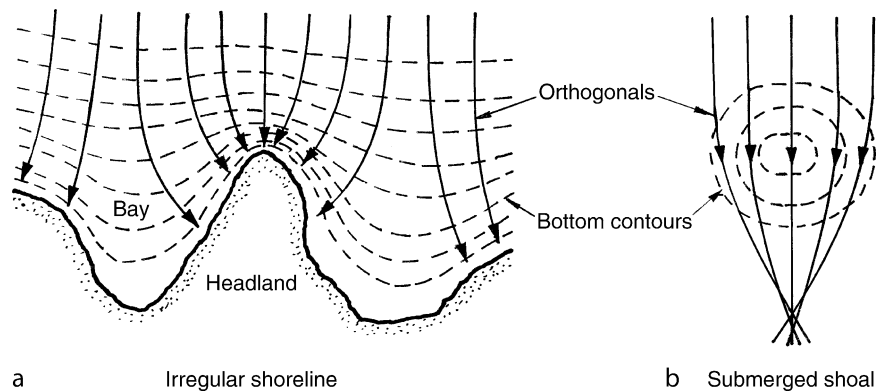
Essentially, the reef acts as a lens focussing the wave energy. If the energy is focussed off the reef, i.e., similarly to Figure 4b, then it is not possible for a cay to form on that reef. However, if the shape and orientation of a reef are favorable, the energy will be focussed on the reef platform toward its leeward side (Figure 5a). Stable cays form when the long axis of the reef lens is aligned with the dominant wave direction and the refraction pattern also does not change much with changing ocean wave direction or period. However, it is virtually impossible for a stable cay to form on a circular reef (Figure 5b), since changes



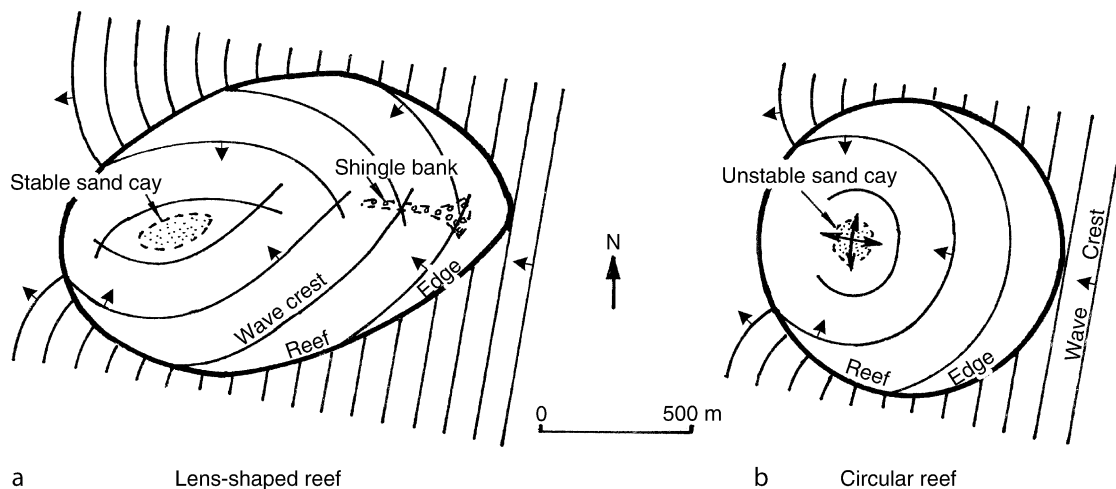
**Wave Shoaling and Refraction, Figure 3** Refraction of waves at a step in bottom elevation – derivation of Snell's Law.  $\delta t$  is the time interval during which a wave crest between two orthogonals completes its crossing of the step.

in wave direction and wave period will change the location of the focal zone. Other nonelongated reefs with sharp corners may experience significant changes in the refraction patterns and hence cay locations change when the dominant waves change direction (Figure 6a and b) (see *Infrastructure and Reef Islands*, Figure 9, for the consequences of this cay location change).

Wave interference zones (intersecting orthogonals) also may occur on small reef platforms (Figure 5a). These are generally located on the windward end of the reef platform as waves from either side of the windward end are refracted toward each other. The larger waves breaking on the windward end of the reef are able to move larger detrital material which, if present in sufficient quantities, will form a shingle bank, possibly with a T-shaped head, which in turn may develop into a windward shingle cay.



**Wave Shoaling and Refraction, Figure 4** Refraction of waves at different coastal features. (a) Concentration and dispersion of wave energy along an irregular shoreline. (b) Focussing of wave energy behind a submerged shoal.



**Wave Shoaling and Refraction, Figure 5** Wave refraction on simple reef platforms – effect of reef shape on the formation of cays. Wave period 8 s; reef top water depth 2 m; only every fifth wave crest is shown on reef top (from Gourlay, 1988).

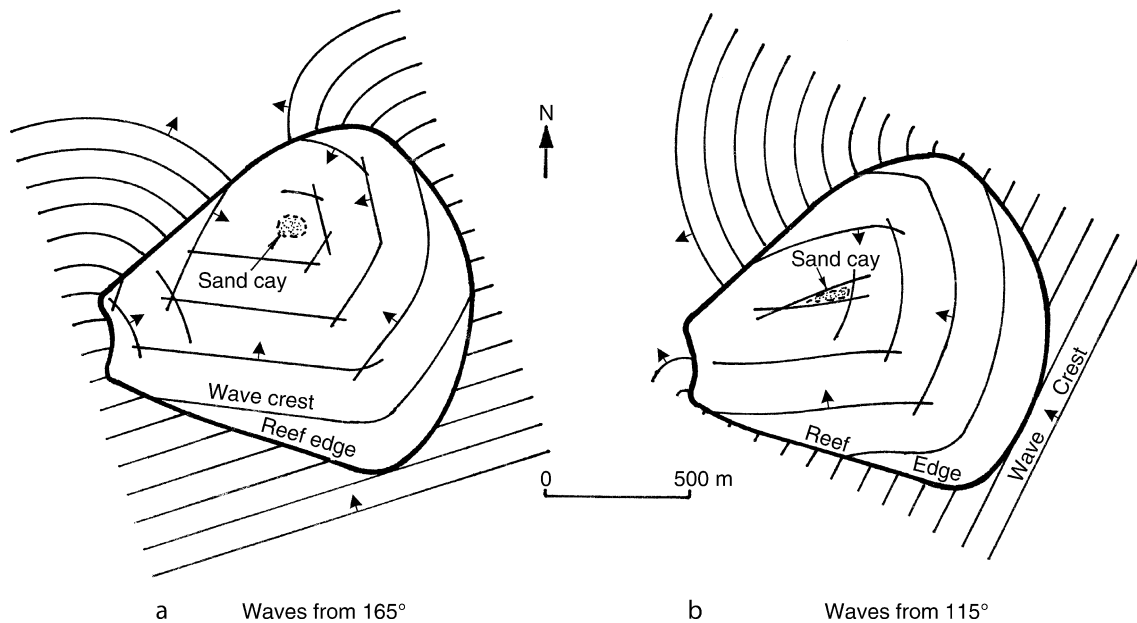
All these processes can be seen in a drawing derived from an aerial photograph of Raine Reef in the outer northern Great Barrier Reef (Figure 7). The axis of this reef is aligned in the NW/WNW – ESE/SE direction which corresponds with the dominant southeasterly trade winds. Water depths around this reef are 200–300 m, so the ocean waves are deep water ones. On this occasion, 9 May 1963, the ocean waves were approaching from the east-northeast. These waves were travelling around both sides of the reef platform, intersecting in deep water behind the reef as both wave trains were diffracted into the sheltered zone there. When the wave crests reached the reef edge, they refracted in the very shallow water on the reef top, changing direction significantly particularly along the southern edge of the reef. After breaking on the reef rim they reformed with much shorter wave lengths and travelled across the reef crest onto the reef flat. Under these typical conditions, an interference zone occurs at the eastern end of the reef but no significant

shingle bank has yet formed there on this reef. However, there is a definite focal zone at the western end of the reef and the large stable cay, Raine Island, is located there. Its shoreline is generally aligned with the refracted wave crests, although there is evidence that these waves might be causing some easterly alongshore sediment movement on the northeastern shoreline of the cay and hence, if this persisted, would reshape the eastern end of the cay. In this case, local shoreline realignment is constrained by beach rock outcrops.

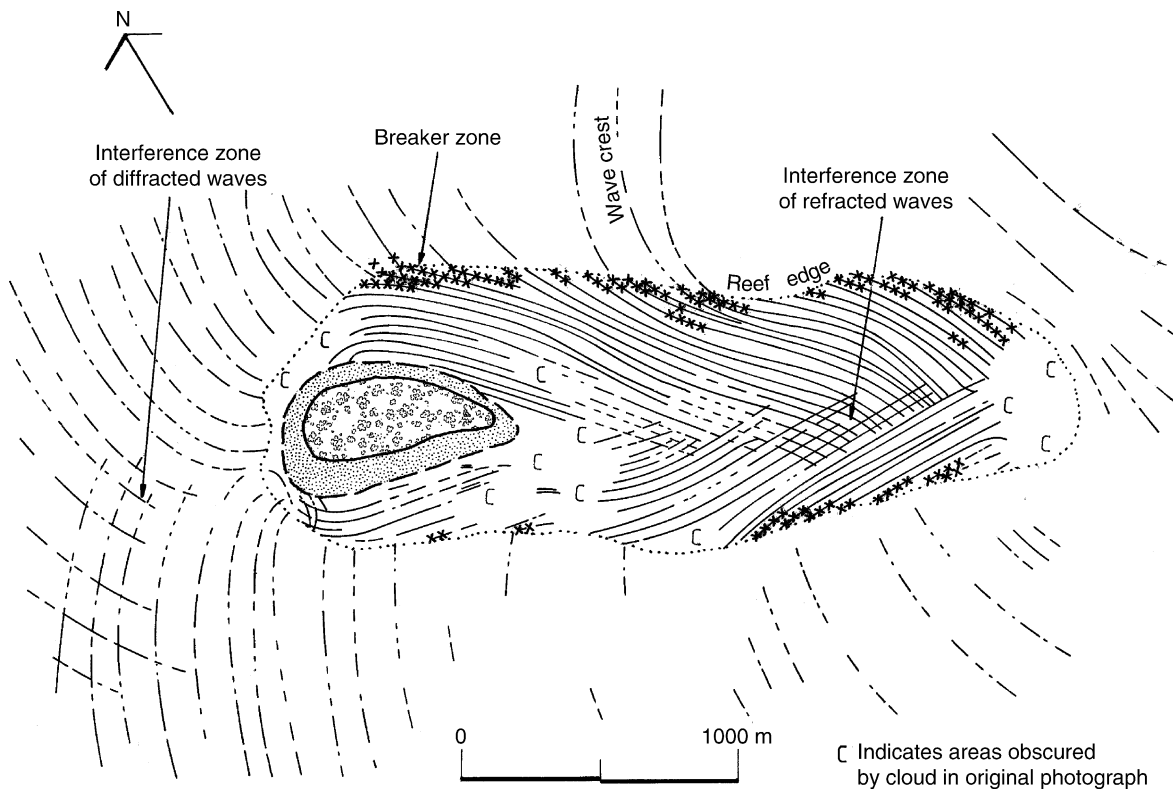
### Summary

The processes of wave shoaling and refraction change the height and direction of waves as they interact with reefs of various shapes and sizes. Significant refraction can occur along the reef edge/rim of an elongated reef aligned with the direction of the approaching ocean waves. As waves break on the reef rim, alongshore currents will transport sediments toward the leeward end of the reef. Diffraction





**Wave Shoaling and Refraction, Figure 6** Wave refraction on simplified form of Gannet Reef, southern Great Barrier Reef – effect of change of wave direction on cay location. Wave period 8 s; reef top water depth 2 m; only every fifth wave crest is shown on reef top (from Gourlay, 1988).



**Wave Shoaling and Refraction, Figure 7** Wave crests on Raine Reef, outer northern Great Barrier Reef, on 9 May 1963 – based on an aerial photograph (from Gourlay and Hacker, 1991, Figure 3.8).

behind the reef will make the sheltered zone behind the reef less sheltered than might be expected. Interference of refracted waves on the reef platform may result in the formation of a windward shingle bank or cay, while sand cays form in the focal zone created by the refracted waves toward the leeward end of the reef. The shape and location of these interference and focal zones vary with changes in wave direction and wave period with consequent modification of the shoreline alignment of cays as their beaches respond to changes in alongshore transport around them.

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## Cross-references

[Cay Formation](#)  
[Coral Cay Classification and Evolution](#)  
[Fringing Reef Circulation](#)  
[Hydrodynamics of Coral Reef Systems](#)  
[Reef Front Wave Energy](#)  
[Wave Set-Up](#)  
[Waves and Wave-Driven Currents](#)

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## WAVES AND WAVE-DRIVEN CURRENTS

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## Definitions

*Sea*. Waves which are being acted upon by the wind that generated them. They are relatively short and steep with short crest lengths. Also called *storm waves*.

*Swell*. Waves which are propagating freely no longer under the influence of the wind that generated them. They are relatively long and flat with long crest lengths.

*Wave celerity C*. The velocity of the wave form. Also known as *phase velocity*.

*Wave height H*. The vertical distance between a wave crest and the following or preceeding wave trough (see Figure 6). Also described as *wave amplitude*  $a = H/2$ .

*Wave length L*. Distance between successive wave crests (see Figure 2).

*Wave period T*. Time interval between the passing of two successive wave crests at a fixed location.

*Wave frequency f* is the inverse of the wave period ( $f = 1/T$ ).

*Orbital velocity*. Velocity of the water particles during the passing of a wave.

*Significant wave height  $H_s$* . Mean height of the highest 33.3% of all waves in a wave record.

*Significant wave period  $T_s$* . Mean period of the highest 33.3% of the waves in a wave record.

*Root mean square wave height  $H_{rms}$* . Wave height which is equivalent to the height of a sinusoidal wave with the same energy as the recorded waves.

See also Chapters *Wave Shoaling and Refraction*; *Wave Set-Up*.

Mathematical symbols are defined where they first appear in the text or on a relevant figure.

The subscript o refers to the deep water values of the various quantities.

The descriptive terms used to describe coral reef morphology vary with the needs and previous practice of the various scientific disciplines. Those used in this entry and related ones (see Chapters *Wave Shoaling and Refraction* and *Wave Set-Up*) are defined in Gourlay and Colleter (2005, pp. 355–356) and in Figure 1 below.

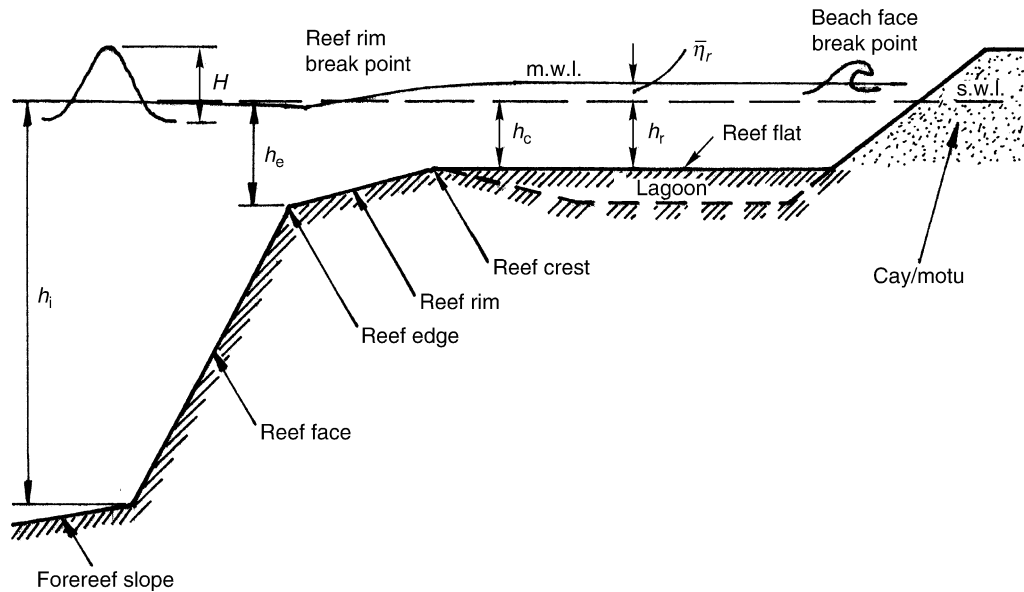
## Introduction

Observations of ocean waves have been made by mariners and engineers for many centuries with empirical relationships being developed for practical use in the nineteenth century when the mathematical study of water waves also began. Scientific study of ocean waves essentially began during World War 2 when knowledge of sea conditions was required at specific locations where amphibious landings were to be made. Coastal engineers developed these new insights about ocean waves in the post World War 2 period using laboratory models and by applying the theoretical and practical knowledge that had been developed during the war. Measurements of ocean waves were first made for engineering purposes such as the design of breakwaters and other structures and for prediction of coastal sediment movements.

During the 1960s and 1970s, oceanographers and earth scientists increasingly built on these foundations with field experiments and new theoretical approaches, while, subsequently, engineers and mathematicians have developed mathematical models based upon these measurements and theories. The study of waves on coral reefs is comparatively recent, with the first significant scientific observations being reported in the mid 1970s (Roberts et al., 1975).

## Ocean waves and coral reefs

Ocean waves are one of the most important physical phenomena shaping the morphology and influencing the ecology of modern coral reefs. Waves passing over shallow reefs agitate the water over the reef surface and modify the flow within the coral matrix. When waves break on the edge



**Waves and Wave-Driven Currents, Figure 1** Definition figure for reef morphology terms.

or surface of a reef the water is aerated; pieces of coral are broken off and transported, together with larvae and other organisms; currents are generated on the reef-top; these wave-driven currents carry organisms and detrital material to other locations. Where planar reef platforms have developed, waves create windward shingle banks and islands, including *Atoll Islands (motu)* and also the sandbanks that develop into leeward *Vegetated Cays*.

There is a large spectrum of waves generated by various causes in the oceans surrounding coral reefs. The shorter period waves are generated by wind blowing over the water surface as various moving weather systems form, grow, and decay. These “wind waves” – sea and swell – have periods from a few seconds to about 20 or more seconds. The predictable tides generated by periodic changes in the gravitational attraction between the earth, moon, and sun are much longer, circa 12 or 24 h (see Chapter *Tidal Effects on Coral Reefs*). The moving weather systems also produce even longer waves such as the storm surge associated with *tropical cyclones (Tropical Cyclone/Hurricane)* and continental shelf waves associated with the passage of larger moving weather systems around large land masses such as the Australian continent. Apparently random events such as landslides and earthquakes may generate *Tsunamis*, long low waves that propagate rapidly over large distances of deep ocean before shortening and amplifying on shallow shelf margins or in confined bays with often disastrous results.

This entry is primarily concerned with wind-generated ocean waves and their transformation as they propagate around and onto reefs and into reef lagoons. As these waves transform and break on reefs they also cause wave-driven currents that are superimposed on the tidal and wind-driven current systems. Indeed in many situations the wave-driven

currents dominate the water circulation system on specific reefs. Important aspects of the reef-top wave system are treated in separate chapters – *Wave Set-Up*; *Wave Shoaling and Refraction*. Comprehensive treatments of the mechanics of water waves are available in Dean and Dalrymple (1991); Massel (1999) and Nielsen (2009).

### Wind-generated ocean waves

When wind blows across the surface of the ocean, that surface becomes unstable, developing small waves that propagate in the general direction toward which the wind is blowing. These waves increase in size as the wind speed increases and reach a maximum size, which depends either upon the duration of the wind event or the distance over which the wind is blowing. The propagation of wind waves over the ocean is governed by gravity, which acts to restore the disturbed water surface to its original smooth condition. Waves that are being acted on by the generating wind are known as sea or storm waves, whereas those that have escaped from the influence of the generating wind are known as swell (see definitions of *sea* and *swell*).

### Wave propagation

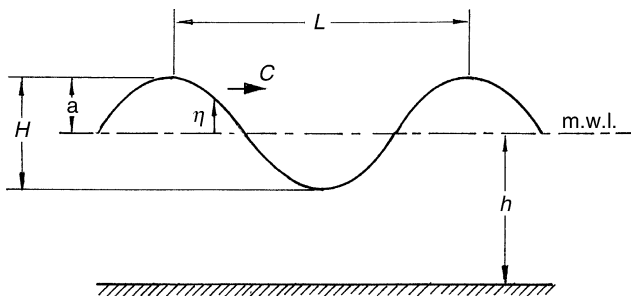
The basic mathematical theory used to represent ocean waves is the small amplitude or Airy wave theory, which represents waves as sinusoidal in form and assumes, among other things, that the wave steepness  $H/L$  is small (Figure 2). In its simplest form this is a linear theory which means that, if more than one wave train is present, the water movement of the resulting wave motion can be obtained by superimposing the water movements of the individual wave trains.



The size of ocean waves is measured in terms of their height  $H$  and their length  $L$  or period  $T$ , where  $L = CT$  (Figure 2).  $C$  is the celerity, which is the velocity at which an individual wave travels over the water surface. Wind-generated ocean waves are oscillatory waves which transmit wave energy across the ocean surface but do not transport water particles with them. Nevertheless, as waves travel across the ocean they cause the water particles to oscillate about a mean position as each wave passes. Oscillatory ocean waves are progressive, that is, they travel in a given direction. However, if they meet an obstacle – a reef, cliff, or breakwater – any of their energy not dissipated at the obstacle will be reflected as a wave traveling in the opposite direction. The superposition of the reflected wave on the original or incident wave will produce a partial or complete standing wave where the water surface oscillates up and down at distances located at half wave length intervals from the reflective obstacle. If the incident wave train approaches the reflective structure at an angle, it will be reflected with the same angle.

Gravity waves propagating in the ocean in most cases are initially deep water waves that propagate without influencing the bottom or being influenced by it. According to small amplitude theory their celerity  $C_0$  increases with their period, i.e.,  $C_0 = gT/2\pi$  and their wave length  $L_0 = gT^2/2\pi$ . This relationship applies when  $h/L_0 > 0.5$ , where  $h$  is the water depth.

As the relative water depth  $h/L$  reduces below 0.5, both the celerity and wave length are increasingly affected,



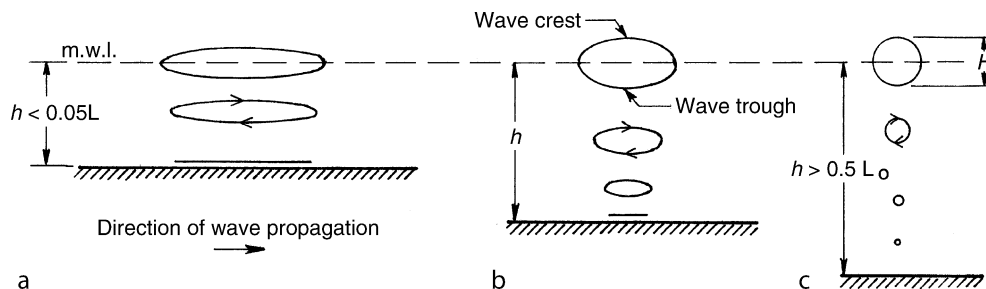
**Waves and Wave-Driven Currents, Figure 2** Definitions of wave height and wave length.

becoming smaller as  $h/L$  reduces, and when  $h/L \leq 0.05$  the waves are shallow water waves with  $C = \sqrt{gh}$ . That is, the wave celerity depends only upon the water depth. The celerity of intermediate depth waves depends upon both the wave period and the relative depth  $h/L$ , where  $L$  also becomes shorter as the depth becomes shallower (see also Chapter *Wave Shoaling and Refraction*).

The type of motion experienced by the water particles disturbed by waves also changes as the waves propagate from deep water into shallow water. In deep water the water particle orbits are circular in form with a diameter equal to the wave height at sea level and decreasing exponentially with increasing depth below that level (Figure 3). When  $h/L \geq 0.5$ , the orbital motion at the bottom is negligible. As waves propagate into increasingly shallow water, the water particle orbits become elliptical in shape with the horizontal motion becoming relatively larger than the vertical motion. In shallow water the horizontal motion is essentially the same at all depths, and there is significant oscillatory water motion at the bottom. In reality individual fluid particles also drift forward in the direction of wave propagation because the positive velocities along the upper parts of their orbits are greater than the negative ones along the lower parts. This process is known as mass transport and the total flow rate per unit length of wave crest generated by it is  $gH^2/8C$  (Nielsen, 2009).

The various formulae for calculating the properties of waves propagating from deep water into intermediate depths involve hyperbolic functions of the relative depth  $h/L$ , where  $L$  is one of the unknown properties. Hence, evaluation of these properties involves iterative calculations or the use of tables of previously calculated values. However, explicit approximations, where the wave properties  $C$ ,  $L$ , etc. are functions of  $h/L_0$ , are now available to simplify these calculations (Nielsen, 2009).

Ocean waves often appear to travel in groups of larger waves followed by groups of smaller waves – fishermen have long held the belief that every seventh or tenth or whatever wave is bigger than the others. Wave theory supports this general idea in that when two wave trains of slightly different wave length travel in the same direction, superposition of their wave forms results in the physical phenomenon known as beats. This involves a periodic variation of the amplitude of the basic wave frequency,



**Waves and Wave-Driven Currents, Figure 3** Wave orbital motion: (a) Shallow water, (b) intermediate depths, (c) deep water.

causing a series of wave groups that move in the same direction as the component waves but at a smaller velocity, the group velocity  $C_g$ .

Wind-generated ocean waves are short waves in that the effect of bottom friction upon their propagation and energy transmission is confined to a thin oscillatory boundary layer immediately above the bottom surface. By contrast, tide-generated waves, storm surges, and tsunamis are long waves in that they are shallow water waves in the ocean, and the effects of bottom friction create a boundary layer extending over the full water depth. Coral reefs generally have much rougher surfaces than most other coastal or shelf bottoms, and it is possible that in some situations wind-generated waves propagating over reefs may have long wave characteristics.

As an ocean wave train propagates across an initially still water surface it deforms that surface and potential energy is stored in the wave form. At the same time, the water particles acquire kinetic energy as they move in their wave-induced orbits. For small amplitude waves the potential and kinetic energies are equal to one another and the total energy per unit water surface area (energy density)  $E = \rho g H^2 / 8$ . Moreover, energy is transmitted in the direction of wave propagation at the group velocity  $C_g$ , which is less than the celerity. Hence, the wave power or energy flux of the wave train,  $P = EC_g$ . In deep water  $C_g = C_o/2$  and so,

$$P_o = \frac{\rho g^2 H_o^2 T}{32\pi}.$$

In shallow water  $C_g \rightarrow C$ .

The linear wave theory, on which the preceding description of ocean waves is based, assumes that surface gravity waves are regular sinusoidal waves of relatively small amplitude, that is, either  $H/L$  or  $H/h$  is small. In reality, ocean waves are neither regular nor have small amplitude. Furthermore, some important wave phenomena, such as wave breaking, wave set-up, and the wave-driven currents the latter generates, can only be explained when nonlinear terms associated with the water motion are considered (see Chapter *Wave Set-Up*).

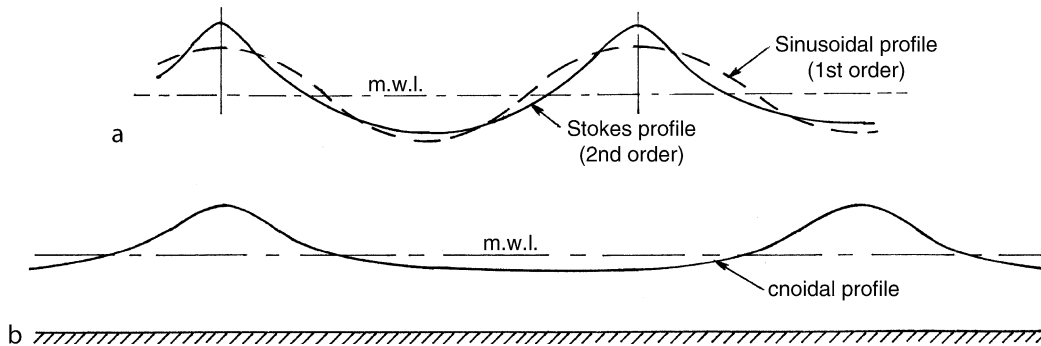
Finite amplitude wave theories give alternative representations of ocean waves when either of the conditions  $H/L \rightarrow 0$  or  $H/h \rightarrow 0$  do not hold, for example, as waves approach the breaking condition. If  $H/L \rightarrow 1$ , Stokes theory with various orders of approximation represents deep water waves. First order Stokes theory is identical with small amplitude wave theory. The second order approximation, that is, including terms in  $H^2$ , has an asymmetric wave profile with the crest amplitude larger than the trough amplitude; crests are sharper and troughs are flatter than sinusoidal small amplitude waves (Figure 4a). It also predicts the mass transport of water particles in the direction of wave propagation. Third order Stokes theory predicts that the wave celerity, which according to small amplitude theory is proportional to the wave period, is also a function of wave steepness.

In shallow water, when the relative depth  $h/L \rightarrow 0$ , a second order solution of the linear shallow water long wave equations results in the cnoidal wave theory. Again these finite amplitude waves have sharp higher crests and flat shallower troughs than sinusoidal small amplitude waves (Figure 4b). Their celerity depends not only on the water depth, but also on the relative wave height  $H/h$ .

Stokes theory becomes increasingly unsatisfactory as waves enter intermediate depths, that is,  $h/L < 0.5$ , while cnoidal theory also is increasingly unsatisfactory as  $h/L$  increases above 0.05. See Nielsen (2009) for further discussion of the applicability of these theories.

### Wave breaking

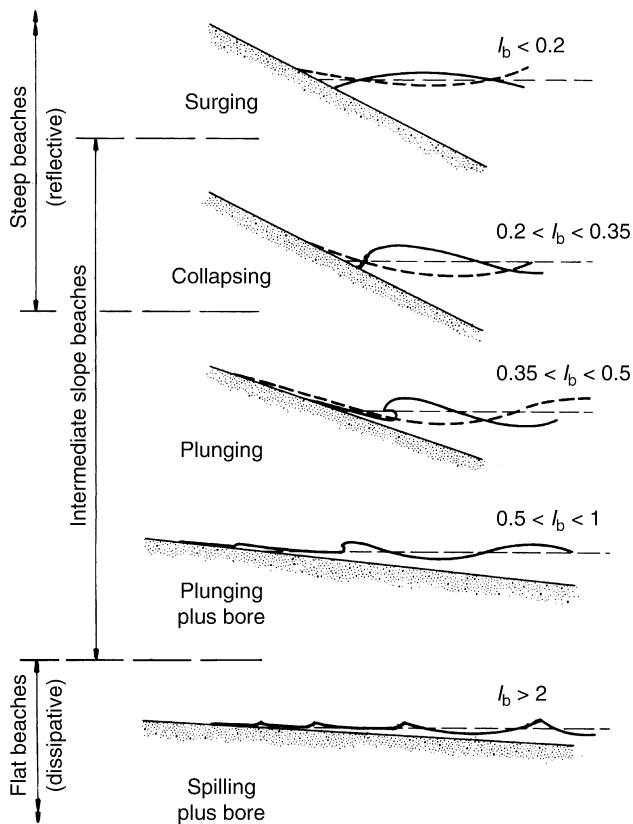
Wave breaking occurs when oscillatory waves become unstable and are transformed into translatory waves that transport water in the direction of wave propagation. This will occur when the horizontal orbital velocity of the water particles at the wave crest exceeds the wave celerity or when their maximum vertical acceleration exceeds the gravitational acceleration. In deep water, ocean waves will break when their wave steepness  $H_o/L_o$  approaches 0.142 (or  $1/7$ ). This process is a gradual one and appears in the formation of increasing numbers of “white caps” on the sea surface as the wave crests spill and develop small rollers on their downwind side. Spilling breakers of similar form



**Waves and Wave-Driven Currents, Figure 4** Wave profiles for finite amplitude waves: (a) Stokes waves in deep water, (b) Cnoidal waves in shallow water.

occur when steep waves break on mildly sloping beaches. Less steep waves breaking on steeper beaches peak up, their forward face becomes vertical, and their crest plunges forward like a jet into the preceding wave trough. On even steeper beaches the lower part of the forward face of the wave becomes vertical and collapses like a partial plunging wave. Surging breakers occur when waves of low steepness break on steep beaches. The forward face of the wave remains relatively smooth and the wave runs up the beach with little foam or turbulence. The uprush–backwash cycle of a surging breaker is completed before the next wave surges up the beach (Figure 5).

The region where waves break is known as the surf zone. It may be divided into three subzones. There is an outer zone where the breaking waves rapidly change shape and develop a surf roller form. Potential energy is transferred into kinetic energy with little loss of energy. In the inner zone the surf roller becomes a bore or moving surge traveling landward over the seaward flowing undertow. Energy dissipation and *Wave Set-Up* occur in this zone. The swash zone occurs on the beach face where uprush and backwash of the breaking waves define the run up and run down limits (see Chapter *Wave Set-Up*, Figure 1).



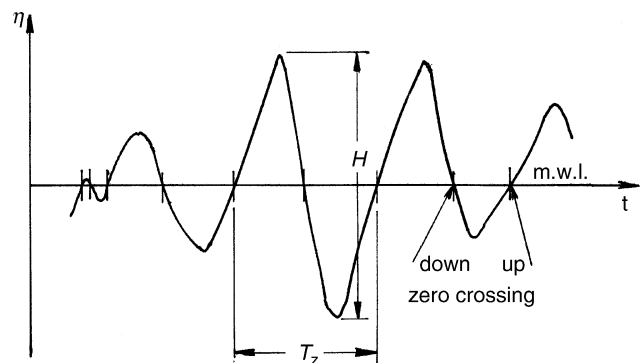
**Waves and Wave-Driven Currents, Figure 5** Beach and breaker types for plane beaches.  $l_b = H_b^{1/2} / g^{1/2} T \tan \alpha$ , where  $H_b$  is breaking wave height and  $\tan \alpha$  is beach slope (reprinted from Gourlay, 1992, with permission from Elsevier).

## Irregular waves

Mariners and others accustomed to observing and experiencing ocean waves have been aware that the periodic regular waves conceived by mathematicians are an inadequate model for wind waves. Visual observations show that the height and period of successive individual waves vary considerably. Moreover, visual observations of wave height have been recognized as giving an estimated wave height somewhere between the actual mean wave height  $H_{av}$  and the largest waves  $H_m$  occurring at the time of observation. The advent of wave recorders produced many short records of a hundred or more waves of different heights and periods. The concepts of significant wave height  $H_s$ , root mean square wave height  $H_{rms}$ , significant period  $T_s$ , and zero crossing period  $T_z$  (Figure 6 and definitions) have been developed to characterize the waves in a given wave record. Statistical theory provides a theoretical wave height distribution – the Rayleigh distribution – which relates  $H_s$ ,  $H_{rms}$ , and  $H_{av}$  to the percent of waves in the record equaling or exceeding a given height.  $H_{rms} (=H_s/\sqrt{2})$  is the wave height equivalent to a sinusoidal wave with the same energy as the recorded waves. The maximum wave height in a given record follows an extreme value distribution, increasing as the number of waves recorded increases.

Using  $H_s$  to characterize the short term statistics of each wave record of say 20-min duration, the long-term statistical occurrence of wave heights can be obtained by using an exceedance plot for  $H_s$  at a given location, in which a given value of  $H_s$  is plotted against the percent of time it is equalled or exceeded. However, a more fundamental and physically meaningful long-term wave statistic would be one based upon the maximum value of  $H_s$  during various independent storm events.

The sea surface is continually changing. Since the wave celerity in deep water depends upon the wave length or wave period, the various waves present are continually moving in and out of phase with each other. The resulting sea surface is quite irregular and often consists of alternating groups of high and low waves. Moreover, the highest waves do not persist but are randomly distributed in space



**Waves and Wave-Driven Currents, Figure 6** Definitions of wave height and period ( $T_z$ ) in a record of irregular ocean waves.

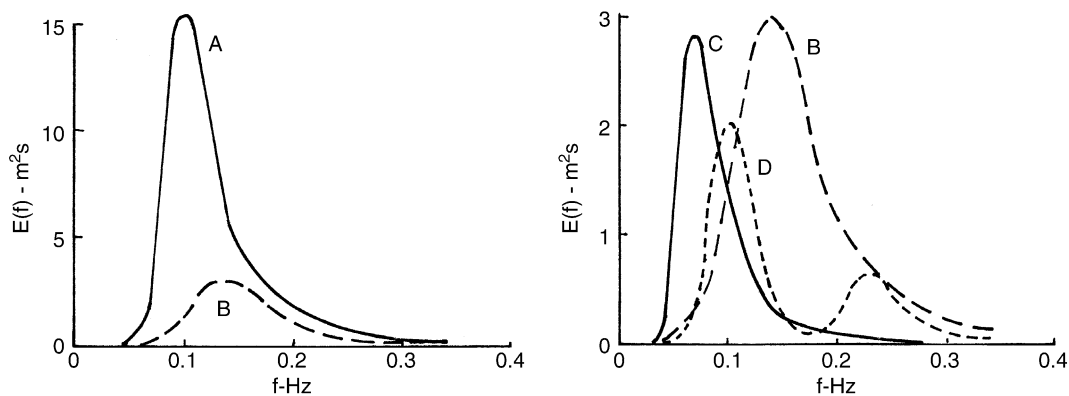


and time. Such a sea surface can be approximated by the superposition of a large number of small amplitude wave trains from different directions. This leads to the concept of the wave spectrum in which the energy associated with a given frequency band has been determined for the full range of frequencies present in a given wave record (Figure 7). If the area under the wave spectrum diagram is designated as  $m_0$ , it can be shown that  $H_s = 4\sqrt{m_0}$ , so measurement of the wave spectrum gives an alternative estimate of the significant wave height  $H_s$ . The period  $T_p$ , corresponding to the peak of the frequency spectrum, is commonly used as the characteristic period for a given wave condition.

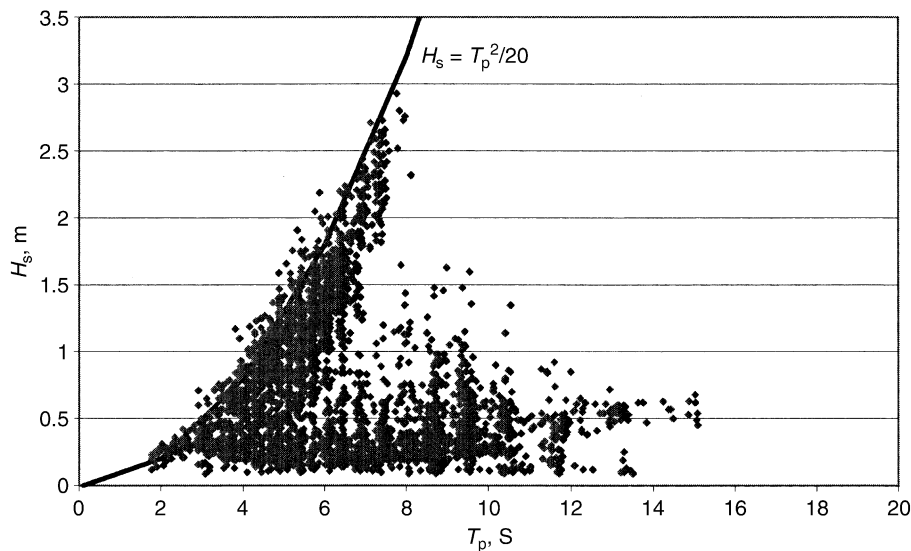
For wind-generated storm waves, the spectrum is broad, and  $T_p$  corresponds with a celerity approaching

the wind speed generating the waves. Swell waves have narrower spectra and larger values of  $T_p$  than storm waves. In open ocean and other situations, where locally generated wind waves are superimposed upon underlying swell, the wave spectra will have at least two peaks and hence two values of  $T_p$  (Figure 7).

A useful means of showing the variation of ocean wave conditions at a given location for a period of time is an  $H_s$ – $T_p$  scatter diagram (Figure 8). Such a diagram commonly will show an upper limiting curve where  $H_s \propto T_p^2$ , representing the maximum wind waves (sea) that can be generated at that site. In open waters this diagram also has a long tail with relatively low  $H_s$  but increasing  $T_p$  representing swell that has come from distant storms.



**Waves and Wave-Driven Currents, Figure 7** Ocean wave spectra (minor irregularities of spectral profiles have been removed) (A) Storm waves  $H_{os} = 4$  m,  $T_p = 9.5$  s; (B) wind waves  $H_{os} = 2.1$  m,  $T_p = 7$  s; (C) swell  $H_{os} = 1.7$  m,  $T_p = 14$  s; (D) sea and swell  $H_{os} = 1.5$  m,  $T_{p1} = 10$  s,  $T_{p2} = 4.4$  s.



**Waves and Wave-Driven Currents, Figure 8**  $H_{os}$  vs.  $T_p$  scatter diagram for ocean waves on southern side of Heron Reef, southern GBR: November 1996 to March 1997 (from Gourlay and Hacker, 2008a, p. 111).

### Wave transformation on reefs

"The interaction of physical processes with coral reefs is complex; each reef system has its own unique set of environmental and morphologic conditions" (Roberts et al., 1975, p. 234). The characteristics of ocean waves depend upon the climatic conditions generating them, and their transformation as they propagate over reefs is significantly influenced by the morphology of the reef system and adjacent or adjoining land masses. Moreover, wave transformation and accompanying wave driven-currents occur in water depths that vary with the periodic water level variations caused by the tides. Hence, the wave driven-currents are superimposed upon and interact with those generated by the tides, as well as with wind-driven currents. Climate, reef morphology, and tides all vary in different parts of the world and so do wave interactions with local coral reefs.

Reef morphology may vary from relatively wide fringing reefs with a flat seaward face fronting a beach to a narrow strip of steep-faced reef backed by a lagoon with a beach or reef behind it. Offshore reefs may be two-dimensional barrier reefs or three-dimensional island reefs usually with steep faces. Atolls have relatively narrow reefs with steep faces, enclosing a lagoon of sheltered water. Narrow reef islands (motus) prevent waves reaching the atoll lagoon except through the gaps in between the islands or passages through the reef. Some reefs are submerged at all times, and in many cases the coral growth on their surface provides a rough porous matrix which interacts strongly with the waves. In other cases reefs have reached the sea surface and have developed relatively smooth planar reef tops with different zones: smooth coralline algae, coral with many depressions but few projections, and even sandy reef flats. Where there is significant tidal variation of water levels the planar reef surface is generally at about the same elevation as the mean low tide level.

Several types of waves break on or travel around or across reefs. First, there are wind waves and swell from the surrounding ocean. Then there are short period waves, locally generated in shallow lagoons on the reef top or in larger deeper lagoons of atolls. Waves breaking on the reef rim release both shorter (secondary) waves and longer (infragravity) waves that alter the properties of waves traveling across the reef top.

Wave transformation over a reef varies depending upon which part of the reef is under consideration. Five zones can be distinguished. These are as follows:

- (1) The outer reef face where waves are affected by shoaling water but may not break
- (2) The reef edge where the larger waves generally break
- (3) The reef rim, between the reef edge and the reef crest, where smaller waves break and the breaking surge dissipates most of its energy
- (4) The reef flat or lagoon where the waves reform
- (5) The beach of either a reef island, continental island, or mainland, where the reformed waves finally break

On the outer reef face waves are subject to the processes of *Wave Shoaling and Refraction*. However, reef face slopes are very variable and so are their effects on waves. In some cases such as the ribbon reefs on the outer northern Great Barrier Reef (GBR) the reef face is almost vertical (Young, 1989). In these situations the effects of refraction and shoaling before breaking will be small, but significant reflection of wave energy may occur. Energy dissipation prior to breaking will be negligible but the actual breaking action on the reef edge will be very intense. Both field and laboratory observations indicate that on reefs with very steep faces the type of breaker is different from those observed on normal sloping beaches, being neither a plunging breaker nor a spilling breaker. The waves do not peak up significantly before breaking nor do they plunge but rather collapse into the strong backwash flowing seaward from the reef top.

On the flatter seaward faces of the Caribbean fringing reefs the bottom is much more irregular than on a sandy coast, and so significant energy dissipation may occur before the waves break (Roberts et al., 1975). Even where the reef face is steep but the water depth over the reef crest is relatively small, breaking waves may shape the seaward side of the reef crest into a ramp with a slope of the order of 1 in 8 to 1 in 15 where the waves break and dissipate a significant amount of energy before the breaking surge reaches the reef crest. In other situations the seaward part of the reef rim may develop a particular morphology created by the interaction between the waves and the growing reef structure. This is the characteristic spur and groove system (*Spurs and Grooves*) often found on the windward edges of reefs.

Normally waves break on the reef rim unless the water depth over it is large. For any given water depth over the reef the wave height on the reef increases with increasing ocean wave height up to a maximum limiting value. Thereafter, any further increase in ocean wave height does not increase wave heights on the reef. Indeed they may even reduce somewhat (Kono and Tsukayama, 1980). In some situations waves will pass over the reef rim at higher tide levels and travel across the reef flat or through the reef lagoon without breaking until they reach a cay or mainland beach where they finally break. Submerged reefs may only experience breaking wave conditions with large waves, and all wave action may pass over the deeper reefs without any breaking.

The width of the surf zone on the rim of a near horizontal reef is of the order of a few wave lengths. Laboratory data (Nelson and Lesleighter, 1985; Gourlay, 1994) show that the initial breaking process on a reef with a steep face is completed within one wave length from the reef edge. The distance from the reef edge to the end of the surf zone where the waves reform varies from three wave lengths upward depending upon the ratio between the ocean wave height and the water depth over the reef. For typical conditions within the GBR region, for example, waves of 3 m height and 6 s period breaking on a reef with 2 m of water over it, this zone would be 100–125 m wide. In exposed conditions on the outer barrier with a 3 m swell of 10 s

period in the same water depth the surf zone would be 160–200 m wide. Extreme waves of 8 m height and 10 s period in the same depth would create a surf zone 300–400 m wide.

The height of the reformed waves at the leeward side of the surf zone is limited by the water depth. Field studies at John Brewer Reef in the central GBR indicate that after the completion of wave breaking the maximum significant wave height is 0.35–0.4 times the water depth over the reef flat and that the maximum wave height in most cases does not exceed 0.6 times the water depth (Hardy and Young, 1996). Laboratory data (Nelson, 1987; Gourlay, 1994) confirm that the maximum  $H/h$  value for waves propagating over horizontal bottoms or very flat slopes is about 0.55. However, higher order approximations of nonlinear wave theories indicate that, when waves propagate in water of constant depth, the maximum possible value of  $H/h$  is close to 0.78. This value is commonly used in coastal engineering practice to determine where waves break on beaches outside coral reef regions. When the presence of higher harmonics generated on a horizontal bottom or at an abrupt depth change is considered, wave theory predicts a maximum  $H/h < 0.6$  (Massel, 1996).

Field observations on various reefs in different parts of the world show that waves are very much changed as they travel across a reef flat. Not only do wave heights become smaller because of breaking and frictional resistance but the wave spectrum broadens as energy is transferred to both higher frequencies (shorter periods) and lower frequencies (infragravity waves). Breaking waves are highly nonlinear, and secondary waves, which are harmonics of the primary wave period, develop during the shoaling and breaking process. Consequently, the reformed waves generally have shorter periods than the incident ocean waves as the primary wave and one or more secondary waves travel across the reef (Figure 9). This may be particularly the case for long swells (Wiegel, 1990). The lower frequency infragravity waves are responsible for the surf beat that causes fluctuations in the mean water level (dynamic set-up) in the surf zone (see Chapter *Wave Set-Up*). Where water is ponded on the reef flat at low tide, local winds may generate short period waves ( $1 < T < 3$  s) on the ponded water.

Significant energy losses occur as waves propagate across coral reefs. Observations in both the field and laboratory models indicate that the energy dissipation of waves breaking on coral reefs varies between 72 and 97% of the incoming wave energy (Roberts et al., 1992; Gourlay, 1994; Brander et al., 2004). This energy dissipation is caused by both bottom friction and wave breaking (Gerritsen, 1981). As reef surfaces are much rougher than those of sandy beaches by a factor of at least 10–20 times (Nelson, 1996), a relatively greater proportion of energy dissipation over coral reefs is caused by bottom friction. With relatively small waves passing over a shallow reef, friction dissipates a larger proportion of the wave energy than wave breaking (Lowe et al., 2005). Bottom friction also will have a relatively greater effect than wave breaking



**Waves and Wave-Driven Currents, Figure 9** Multiple crested secondary waves on reef flat, Rarotonga, Cook Islands, South Pacific Ocean. Photo: Michael Gourlay, March 1995.

on flatter reef face slopes and wider reef flats. As the size of the waves increases the proportion of wave energy dissipated by breaking increases, and eventually dissipation by wave breaking will dominate when waves are large.

While the beaches of reef-protected shorelines vary in form from place to place, these beaches are often relatively steep ( $\tan \alpha > 0.1$ ) with a plane face and are formed of medium to coarse coral sand. At low tide, no waves reach the beach since the waves break on the reef rim. However, as the tide rises, some reformed waves travel across the reef flat or shallow lagoon and break directly on the beach face. If these waves are steep ones they will plunge onto the beach and their energy will be dissipated in the uprush–backwash cycle on the upper beach face. If, on the other hand, waves of low steepness, such as long swells, pass over the reef rim and the reef flat without decomposing into secondary waves, the breakers will surge up the beach with little energy being dissipated. The latter waves have considerable potential to overtop the beach crest and move sand landward, so increasing the height of the beach crest. Moreover, on narrow reef flats the longer period infragravity waves can produce resonant oscillations of water level, which dominate the wave uprush process on a reef-protected beach (see Chapter *Wave Set-Up*).

In a study based upon three coral reefs with different morphologies and hydrodynamic (wave and tidal) conditions, Kench and Brander (2006) found that the effect of incident wave energy in reshaping reef-protected beaches depends upon a reef energy window index  $\psi = (\text{mean reef flat water}$



depth at high spring tide)/(reef width). A narrow reef width with a low reef flat elevation has a large value of  $\psi$ , indicating that more wave energy will cross the reef and break on the island shoreline, whereas a wide reef with a high reef flat elevation has a low value of  $\psi$ , indicating that most wave energy will be dissipated on the reef rim and relatively little of it will reach the island. Rising sea levels and disintegration of reef top corals following coral bleaching events have the potential to increase the depth of water over a reef flat, thus increasing  $\psi$  and making reef islands more vulnerable to erosion (Sheppard et al., 2005).

In the tropical latitudes where coral reefs flourish, winds and waves vary seasonally. For example, South Maalhosmadulu Atoll in the Maldives lies at latitude 5°N. It is subject to both westerly and northeasterly monsoon conditions with the former lasting longer (8 months) and also producing greater incident wave energy on the atoll and its reefs than the latter. Underlying swell from the south also refracts around the atoll delivering greater energy to its western side, independently of monsoon conditions. On an atoll scale these seasonally changing wave energy conditions control the formation, shape, and location of reef islands on the various small reefs forming the atoll, whereas on a reef scale they cause seasonal fluctuations in the positions of island beaches (Kench et al., 2006). Waves on the windward sides of reefs and cays are generally larger and shorter than those on the leeward sides, resulting in higher windward reef flat and beach ridge elevations (Kench et al., 2009; Samosorn and Woodroffe, 2008).

At Raine Reef, one of the outer reefs of the northern GBR (latitude 11° 36' S), southeasterly trade winds dominate during the winter months and northwesterly monsoon winds occur during most summers. Swells from distant tropical cyclones in the Coral Sea also reach this reef during summer, and occasional, generally small, tropical cyclones may affect it directly. Wave transformation across this relatively small reef platform is very much a three-dimensional process (see Figure 7 in Chapter *Wave Shoaling and Refraction*) and has resulted in the formation of a large cay located at the leeward end of the reef under the influence of the dominant southeasterly waves. Northwesterly monsoon waves transport sediment eastward along the northern beach, often creating a recurved sand spit at the eastern end of the island. During the subsequent winter southeasterly waves transport much of the sand from this spit along the southern shore of the island to its southwestern corner. Hence, seasonal variations in winds generate waves that cause a clockwise movement of sand around this reef island.

Many of the field experiments involving waves breaking and propagating across coral reefs have been undertaken at relatively sheltered locations or at times of low energy conditions. The duration of measurements in most cases is no more than a week or two. Conclusions based upon the experimental data obtained from such experiments may not be valid when more energetic conditions, that is, cyclonic/hurricane wave conditions, occur. In many cases significant sediment movement and morphological changes on reefs or reef-protected shorelines only occur during

extreme events and even then only when reef top water levels are elevated above normal levels by wave set-up, high tides, storm surge, or tsunami.

### Wave-driven currents

Surfers and fishermen have been aware for a long time of the existence of wave-driven currents, such as alongshore currents, rip currents, and undertow, within the surf zone of beaches. Earth scientists and engineers concerned with coastal structures also have been aware of the transport of sand and gravel along coasts by waves and the problems this transport can cause when breakwaters are constructed to form new harbors or to stabilize river entrances. However, it was not until mathematical physicists such as Longuet-Higgins and Stewart (1964) extended the sinusoidal (small amplitude) wave theory to include the concept of wave thrust or, as they described it by analogy with electromagnetic waves, radiation stress, that a proper scientific understanding of the mechanism driving the various surf zone currents was developed. This theoretical analysis also predicted that the waves would produce changes in the mean water level as they approached a beach: wave set-down offshore of the surf zone and wave set-up within the surf zone (see Chapter *Wave Set-Up*).

Initially wave-driven current systems were observed on fringing reefs on various islands in the Caribbean and Pacific regions. In some locations the reefs were relatively narrow and were backed by lagoons so that the reefs functioned as submerged breakwaters. At Grand Cayman Island in the Caribbean the waves discharged water over the reef rim into the lagoon where it flowed parallel to the reef crest and shoreline and discharged seaward through a channel at the end of the reef (Roberts et al., 1975; Roberts, 1981). Similar wave-driven current systems were observed at Guam in the northern Pacific Ocean where the water returned to the ocean through channels in the reef rim, associated with rivers (Marsh et al., 1981). Tidal ranges were generally less than 1 m.

The extensive Ningaloo Reef is located in the Indian Ocean on the edge of the continental shelf close to the Western Australian coast. Waves breaking on this westward-facing reef were observed to generate a landward flow across the reef with return circulation in the lagoon between the reef and the mainland. Water returned seaward through channels through the reef north and south of the inflow zone. The spring tide range was almost 2 m (Hearn et al., 1986).

In most of these cases, waves breaking on the reef rim transport water landward across the reef flat into shallow lagoons between the reef and the mainland. The flow then runs parallel to the shoreline until it reaches a gap in the reef or the end of the reef, where it flows seaward back to the ocean. Where the outflowing current is sufficiently strong, sediments on the reef flat or lagoon bottom are likely to be transported offshore and deposited in deep water sinks from which they cannot be returned to the reef system (Roberts, 1981). Navigation channels dredged

through the rim of coral reefs always carry this risk, unless specific action is taken to prevent it occurring. The boat access channel at Heron Island in the southern GBR is an example of this type of situation (Gourlay and Hacker, 2008b) (see Chapter *Infrastructure and Reef Islands*).

On offshore barrier or platform reefs, waves breaking on the windward reef rim transport water across the reef flat either over the leeward reef rim or in the case of atolls into the lagoon behind the reef. Such currents have been observed at John Brewer Reef and other locations in the GBR system (Young, 1989; Hardy et al., 1991). The velocities of these wave-driven currents have been found to be approximately proportional to the height of the waves causing them (Hearn and Parker, 1988; Symonds et al., 1995).

When waves approach the reef rim at an angle, they will be refracted as they travel across the sloping reef face and break either there or on the reef rim. Breaking waves that cross the reef rim at an angle will generate an alongshore current similar to that generated when waves break at an angle to a beach (see Chapter *Wave Shoaling and Refraction*). The actual directions of flow of wave-driven currents on reef tops depend upon several factors, including the direction of the ocean waves relative to the reef platform, the water depths over the reef top, the reef morphology, the roughness of various zones on the reef, etc. In general, currents flow from the breaker zones where wave set-up is highest to the lower portions of the reef top or to gaps in the reef surrounding a lagoon.

Laboratory models of small platform reefs in the GBR demonstrated these principles quite clearly (Gourlay, 1993; 1995). A model of Raine Reef on the northern outer barrier showed how wave set-up at the windward eastern end of the reef drives a current down the center of the reef and around the coral cay at its leeward end. A model of North Reef in the southern Capricorn region showed how the presence of a windward shingle bank obstructs the longitudinal flow, particularly at low tide levels, forcing it to follow a path defined by the lower levels on the reef top.

### Modeling wave-driven flow across reefs

Researchers modeling wave-driven flow across reefs have assumed a two-dimensional reef profile with a seaward sloping reef face and a horizontal reef top. Waves break on the sloping reef face, dissipating their energy and generating wave set-up. The maximum set-up  $\bar{\eta}_r$  occurs at or near the reef edge, that is, at the seaward side of the horizontal reef top. This maximum set-up creates the pressure gradient required to drive the wave-driven flow across the reef top since the water level at the downstream side of the reef is assumed to be the same as that seaward of the surf zone. The various approaches for modeling wave-driven flow across reefs have been reviewed by Gourlay and Colleter (2005) and Monismith (2007).

The mathematical models are based on the depth-integrated (one-dimensional) equations of motion for steady free surface flow, that is, the momentum equation incorporating the wave thrust, and the continuity equation.

The various researchers make different assumptions in applying these equations to wave-driven flow across a reef. Symonds et al. (1995) assume that  $\bar{\eta} \ll h$  at all places, that is, the set-up is not included in the water depth so  $\bar{\eta} + h$  is replaced by  $h$ . They also assume that the breaking wave height is linearly related to the depth at the break point and that this ratio  $\gamma$  is the same throughout the surf zone and on the reef top. Their friction term is a linear function of the wave orbital velocity, and there is no shoaling or friction offshore of the break point. In contrast, Hearn (1999) does not assume that set-up is small in comparison to the water depth. Furthermore, he assumes that the breaker index  $\gamma$  has different values at break point, in the surf zone, and on the reef top. He also ignores friction both offshore and in the surf zone, but considers the very significant effect of large reef top roughness in creating frictional resistance to the wave-driven flow. Massel and Brinkman (2001) extend the model of Symonds et al., using a more detailed representation of the breaking process, while Lugo-Fernandez et al. (2004) allow for a continuous decrease in wave height across the submerged reef crest.

The model of Symonds et al. produces a simple analytical solution with the friction coefficient only occurring in the scaling parameter for velocity, so the magnitudes of both the wave set-up and the sea surface slope across the reef top are independent of friction. Their solution predicts a reduction in set-up when there is a flow across the reef but it can not give meaningful results when ocean tide levels approach reef top elevation, that is, when  $\bar{\eta} \geq h$ , nor for steep-faced reefs when waves break directly on the reef edge. Hearn's model predicts that the wave set-up is identical to that predicted by Tait (see Chapter *Wave Set-Up*) and that its magnitude is unaffected by the flow. The models of both Symonds et al. and Hearn qualitatively agree with Gourlay's laboratory experiments in that the velocity  $V_r$  of the wave-driven flow over a reef increases from zero when the ocean water level rises above reef top level, increasing to a maximum with increasing water depth and then decreasing as wave breaking and hence wave set-up reduce, finally becoming zero again when the depth on the reef top equals/exceeds the depth at which waves pass over the reef without breaking. Hearn showed that some deeper reefs, for example, Kaneohe Bay, are in the regime of decreasing wave breaking, and hence the current velocity reduces with increasing water depth while many shallower reefs, e.g., Ningaloo, are in the regime in which the current increases with increasing depth.

Overall, these approaches are restricted to reef situations where the reef face slopes are relatively flat and waves generally break a significant distance seaward of the reef crest. Moreover, their results may not be meaningful for very shallow water depths over the reef top. Terms involving  $V_r^2$ , representing the friction and kinetic energy of the current, are not always considered.

Various researchers, for example, Kraines et al., 1998; Angwenyi and Rydberg, 2005, have applied these or

similar approaches to numerical models of specific sites, involving reefs and bays, where wave-driven currents are superimposed upon the dominant tidal current circulation.

### Wave pumping

Another approach to wave-driven currents on coral reefs is the wave pump analogy. An early presentation of the wave pump was given by Bruun and Viggoson (1977). Essentially, the waves breaking on the reef rim act as a pump lifting water from the ocean and discharging it onto the reef top or into the lagoon behind the reef. The water pumped onto the reef or into the lagoon then flows back to the sea over the leeward side of the reef in accordance with open channel flow theory. The directions of flow on the reef top will be controlled by the reef morphology with flows tending to concentrate at the lower portions of the reef rim or in channels through the reef enclosing the lagoon. The wave pump is most efficient on steeper faced reefs.

As explained in the Chapter *Wave Set-Up*, waves breaking on the reef face/rim raise the mean water level in the reef top surf zone above the ocean water level. If this water cannot escape, the mean water level surface, or wave set-up, over the reef top landward of the surf zone is horizontal, and the only return flow to the ocean is the backwash over the reef rim between breaking waves. Such a situation rarely occurs in nature but can be easily simulated in the laboratory. Where the water can escape over a portion of the reef rim behind the surf zone then it will flow toward that area. As it does so, some of the potential energy of the wave set-up will be converted into kinetic energy (proportional to  $V_r^2/2g$ ) and the reef top wave set-up will be reduced by this amount. Furthermore, the flow of water on the reef top will be resisted by friction on the relatively rough reef surface, and this will dissipate an increasing

amount of energy as the distance between the surf zone and the leeward side of the reef increases. This energy dissipation by friction will be accompanied by a fall in the mean water level in the direction of flow.

The basic processes of the wave pump generating wave set-up and associated open channel flow across a reef top have been explained through laboratory model experiments in a wave flume (Gourlay, 1996a, b; Gourlay and Colleter, 2005). This model reproduced a steep-faced reef (slope 1 in 1) where waves broke at the reef crest and the resulting current flowed across a horizontal reef top. Following the suggestion of Munk and Sargent (1954), it was found that the wave set-up on the reef was proportional to the wave power or energy flux. Consideration of the conservation of wave power (Figure 10) leads to the following statement

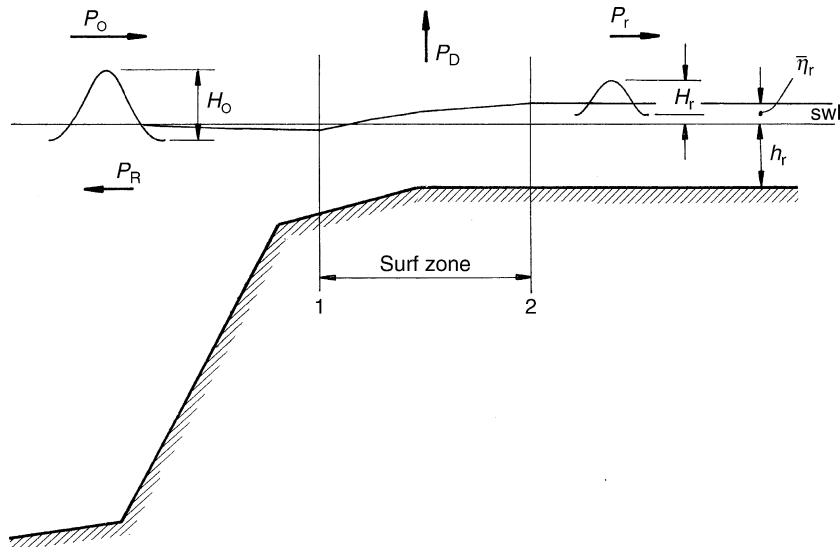
$$P_o = P_R + P_D + P_r + P_v,$$

where  $P_o$  is the ocean wave power approaching the reef,  $P_R$  is the wave power reflected from the reef face,  $P_D$  is the wave power dissipated by wave breaking,  $P_r$  is the wave power transmitted across the reef top, and  $P_v$  is the power of the reef top current.

The various forms of the wave power can be expressed in terms of the ocean wave conditions, the current velocity, and the water depth on the reef top. Subsequent substitution and algebraic manipulation lead to a mathematical expression for the characteristic curves of the wave pump in terms of the following dimensionless parameters:

$$N = f(S, q^*, H_o/L_o),$$

where  $N = \bar{\eta}_r/T\sqrt{gH_o}$  is the dimensionless maximum wave set-up;  $S = d_r/H_o$  is the relative submergence of the reef ( $d_r = \bar{\eta}_r + h_r$ );  $q^* = q/g^{1/2}H_o^{3/2}$  is the dimensionless



**Waves and Wave-Driven Currents, Figure 10** Definitions for wave pump theory for wave-driven flow across a coral reef (reprinted from Gourlay and Colleter, 2005, with permission from Elsevier).



flow per unit length of reef rim;  $H_o/L_o$  is the ocean wave steepness ( $L_o = gT^2/2\pi$ ).

This theory predicts that the wave set-up driving the flow across a platform reef is less than the set-up generated by the same wave conditions on a fringing reef where no flow is generated. When submergence  $S = 0$ ,  $\bar{\eta}_r = -h_r$ , that is the water level  $h_r$  is below the reef top elevation, and the waves are breaking on the reef face. In this case, the maximum value of  $N$  coincides with the dimensionless wave run-up (see *Wave Set-Up*) that just reaches the crest of the rough reef face. No flow across the reef occurs when  $N = 0$  and this occurs when  $S = 2.5$ , which is equivalent to  $H_o = 0.4h_r$ , the condition for waves to pass over the reef without breaking.

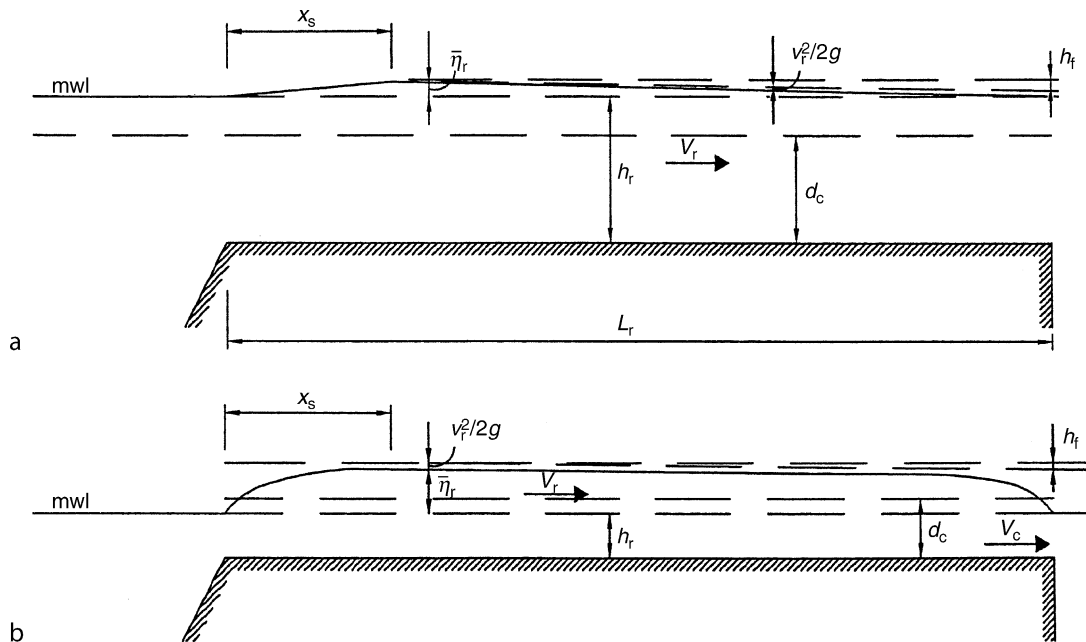
To determine the wave-driven flow on the reef top it is also necessary to know the reef top flow characteristics. The basic equation of motion can be simplified for steady flow in an open channel. Subsequent integration leads to the well-known Bernoulli equation as applied to open channel flow. Consideration of flow energy leads to a condition that indicates that for any given flow there is a particular critical depth at which the flow energy is a minimum. Moreover, there is a larger depth where the flow is relatively slow and deep (subcritical flow) and a smaller depth of fast shallow flow (supercritical flow). In subcritical flow small disturbances can travel both upstream and downstream but in supercritical flow they can only travel downstream.

Wave-driven flows across a coral reef are usually subcritical and are controlled by reef top roughness and downstream water level (reef top control). However, when flow rates are relatively large and/or the falling downstream ocean tide level approaches or falls below the reef

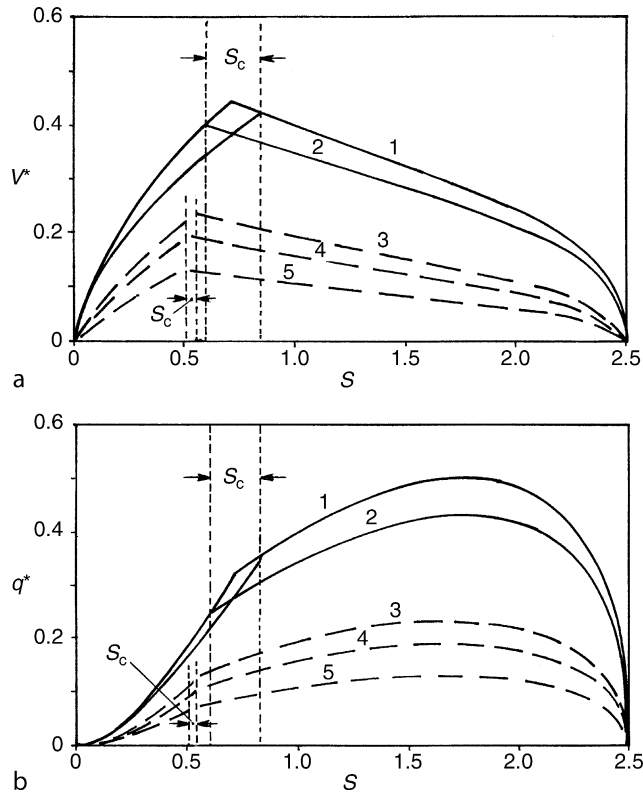
top level, critical conditions will occur on the reef rim and the reef top flow and water levels will be controlled by the downstream reef rim acting as a broad crested weir (reef rim control) (Figure 11).

A combination of the wave pump relationship with open channel flow theory for either reef rim or reef top control leads to analytical relationships for the reef top flow. These relationships allow the development of characteristic curves for a given reef. These characteristic curves show the variation of  $V^*$  ( $= \frac{V_r}{\sqrt{gH_o}}$ ) and  $q^*$  as functions of submergence  $S$ . The reef top characteristic curves are also functions of parameters involving the ocean wave conditions  $H_o$  and  $H_o/L_o$  and the reef top conditions  $K_p, f$ , and  $L_r$ .

Figure 12 shows the reef top characteristic curves for wave-driven flows on the laboratory model and at Heron Island in the southern GBR. There are two basic curves for a given reef, intersecting at a critical value of submergence  $S_c$ . The left hand curve ( $0 < S < S_c$ ) represents reef rim control, that is, the downstream reef rim acts as a broad crested weir; the right hand curve represents reef top control where the flow depends upon the water level difference between the surf zone and the downstream ocean water level, together with the friction factor for the reef top. For given wave conditions the velocity of the wave-driven current is a maximum when  $S$  equals  $S_c$ .  $S_c$  will vary within a relatively small range for a given reef depending upon the wave conditions. In contrast, the maximum flow occurs when  $1.5 < S < 2$ , that is, when the water depth over the reef is relatively large and the flow



**Waves and Wave-Driven Currents, Figure 11** Wave-driven flow across a horizontal reef: (a) Reef top control, (b) reef rim control (reprinted from Gourlay and Colleter, 2005, with permission from Elsevier).



**Waves and Wave-Driven Currents, Figure 12** Reef top characteristic curves for wave-driven flow: (a) Velocity parameter  $V^* = V_r / \sqrt{gH_o}$  versus Submergence  $S = d_r/h_o$ , (b) Flow parameter  $q^* = q / \sqrt{gH_o^3}$  versus Submergence  $S = d_r/h_o$ . Solid line model horizontal reef, broken line Heron Reef, southern GBR: (1) larger waves, (2) smaller waves, (3) cyclonic waves, (4) storm waves, (5) commonly occurring waves.

velocity is less than its maximum possible value. Both  $V_r$  and  $q = 0$  when  $S = 2.5$  when the waves pass over the reef without breaking. As would be expected the narrower, smoother, steep-faced model reef experiences relatively larger velocities and flows than the wider, rougher, flatter faced reef at Heron Island.

The theory for the wave-driven current in the reef top control regime, that is, the right hand part of the reef top characteristic curves, can be simplified to show that, for a given reef:

$$V_r = C_r \left( \frac{H_o T^{\frac{1}{2}}}{d_r^{\frac{1}{2}}} \right) ([1 - 0.16S^2])^{\frac{1}{2}},$$

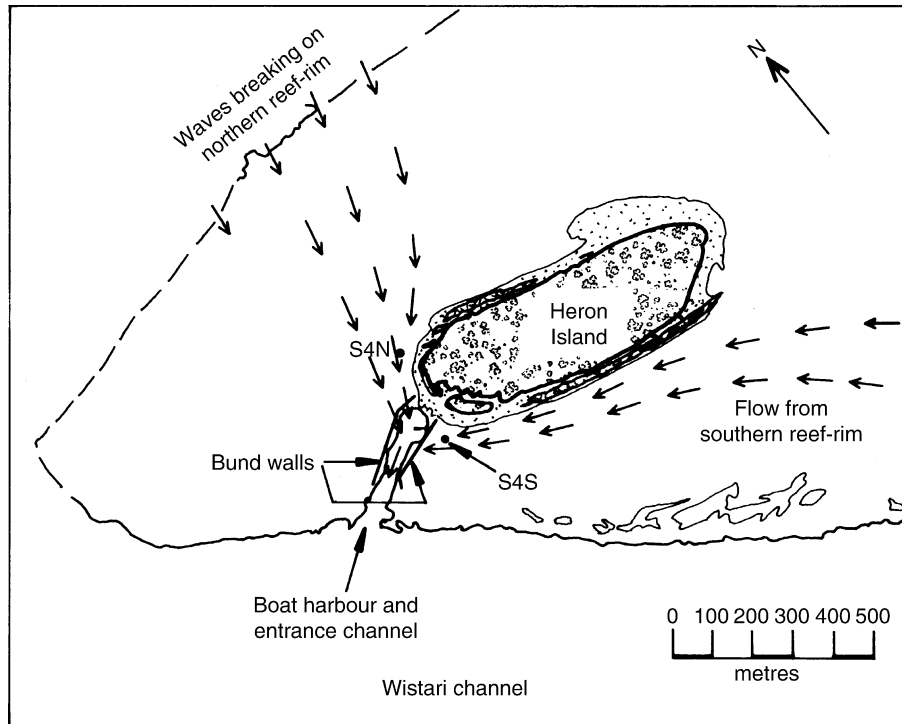
where  $C_r$  depends upon the characteristics of the reef. This equation indicates that the flow velocity is approximately linearly related to the ocean wave height as found by both Hearn (1999) and Symonds et al. (1995), as well as Tartainville and Rancher (2000).

Wave pumping provides a very effective mechanism for flushing atoll lagoons, particularly those that are

completely enclosed by a reef with no channels through its rim. This process has been observed at Manihiki Lagoon in the northern Cook Islands, South Pacific Ocean (Callaghan et al., 2006). Careful measurements of water levels to an accurate common datum showed that the lagoon water level was at all times above the ocean water level, so the ocean tide was not driving the flushing of this lagoon system, even though the lagoon water levels fluctuated with a reduced amplitude in response to the periodic fluctuations in the ocean tide level. Lagoon water levels, averaged to exclude the tidal fluctuations, were found to closely follow the hindcast ocean wave energy flux over a period of several days. Observations on the windward side of the reef confirmed that the breaking waves pumped water on to the reef flat, lifting the water above ocean tide level. On the leeward side of the lagoon water flowed out over the reef rim under critical flow conditions. The wave-driven flow and flushing of the lagoon have been simulated by both analytical and numerical models.

Ocean waves and the reef top currents caused by them at the western end of Heron Reef in the southern Great Barrier Reef were measured over a 12-month period from mid March 1996 to mid March 1997 (Gourlay and Hacker, 2008a, b). Mild conditions, when wind speed was less than 5 m/s and  $H_{os} < 0.5$  m and tidal currents completely dominated on the reef top, occurred over only 45 tidal cycles (7%) during this period, even though the maximum tidal range was greater than 3 m. During the greater part of the year waves influenced the reef top currents at the two measuring sites close to the western end of Heron Island and on either side of the boat harbor and its access channel (Figure 13) (see also Figure 2 in Chapter *Infrastructure and Reef Islands*). Rising tides flowing over the western end of the reef, in through the boat harbor entrance channel and over the harbor bund walls onto the reef flat on either side of the island, were observed to be reversed by wave-driven currents – northeasterly winds/waves reversed currents on the northern side of the island and southeasterly winds/waves reversed currents on the southern side. In some cases, where winds blew along the axis of the island and ocean waves on either side of the reef had similar heights, westward currents occurred along both sides of the island. When waves are sufficiently large ( $H_{os} > 1.5$  m), continuous inflow to the harbor occurs throughout the tidal cycle (Figure 14). For large waves and small tides the westward wave-driven flow varies with the waves rather than the tide. For large tides and smaller waves, the westward flow velocity varies with the tidal cycle and the maximum velocity occurs when weir control develops over the bund walls at low tide. Under commonly occurring wave ( $H_{os} < 1.5$  m) and tidal conditions, the maximum wave-driven currents on the reef top were usually no larger than 0.3–0.4 m/s. However, during the three storm events recorded during this 12-month period ocean waves reached 3 m height and currents were of the order of at least 0.6 m/s (Figure 14).

The observations of wave-driven currents on Heron Reef confirmed the prediction of Gourlay and Colleter's



**Waves and Wave-Driven Currents, Figure 13** Wave-driven flow into Heron Island boat harbor, southern GBR (reprinted from Gourlay and Colleter, 2005, with permission from Elsevier).

theory that the wave-driven current velocity increased with increasing  $H_{os}$  and decreasing reef top water depth. No consistent relationship was found between current velocity and wave period. A direct comparison of measured and calculated current velocities at the northern current meter site for tide levels when the tidal current was zero gives a relationship of the form  $V = C(H_{os} - H_{oscr})$ , where  $H_{oscr} = 0.3-0.5$  m is the threshold condition for a wave-driven current and the constant  $C$  is independent of tidal range (Gourlay and Hacker, 2008b, pp. 222–249). The measured velocities are somewhat lower than the calculated ones, and this could be attributed to the reef top being rougher than it was assumed to be and/or to the ocean wave heights used in the calculation not being reduced to allow for refraction as they propagated from the deeper water surrounding the reef platform onto the shallow reef top.

Most recently Hench et al. (2008), working at Moorea, French Polynesia, have observed wave-driven currents on a coral reef with a shallow lagoon separating it from a continental island and a narrow deep passage connecting the lagoon to the ocean. Tidal ranges during these observations were small (0.3 m), so the water circulation was primarily the result of the set-up caused by waves breaking on the reef. Hench et al. were unable to predict their observed wave set-up using either the theory of Hearn (1999) or that of Gourlay and Colleter (2005), but an empirical relationship was established between wave set-up on this reef and the wave height, wave period, and

the water depth over the reef. Circulation and exchange of water between this coral reef system and the adjacent ocean was largely determined by episodes of larger waves generated by remote weather events rather than periodic tidal exchange mechanisms.

Field measurements of both wave set-up and the levels of the reef and beach topography where they are made must be accurately related to a common fixed land datum. If this is not done, the water depths cannot be determined to sufficient accuracy to reliably compare observed values of set-up and current velocities with those derived from various theories.

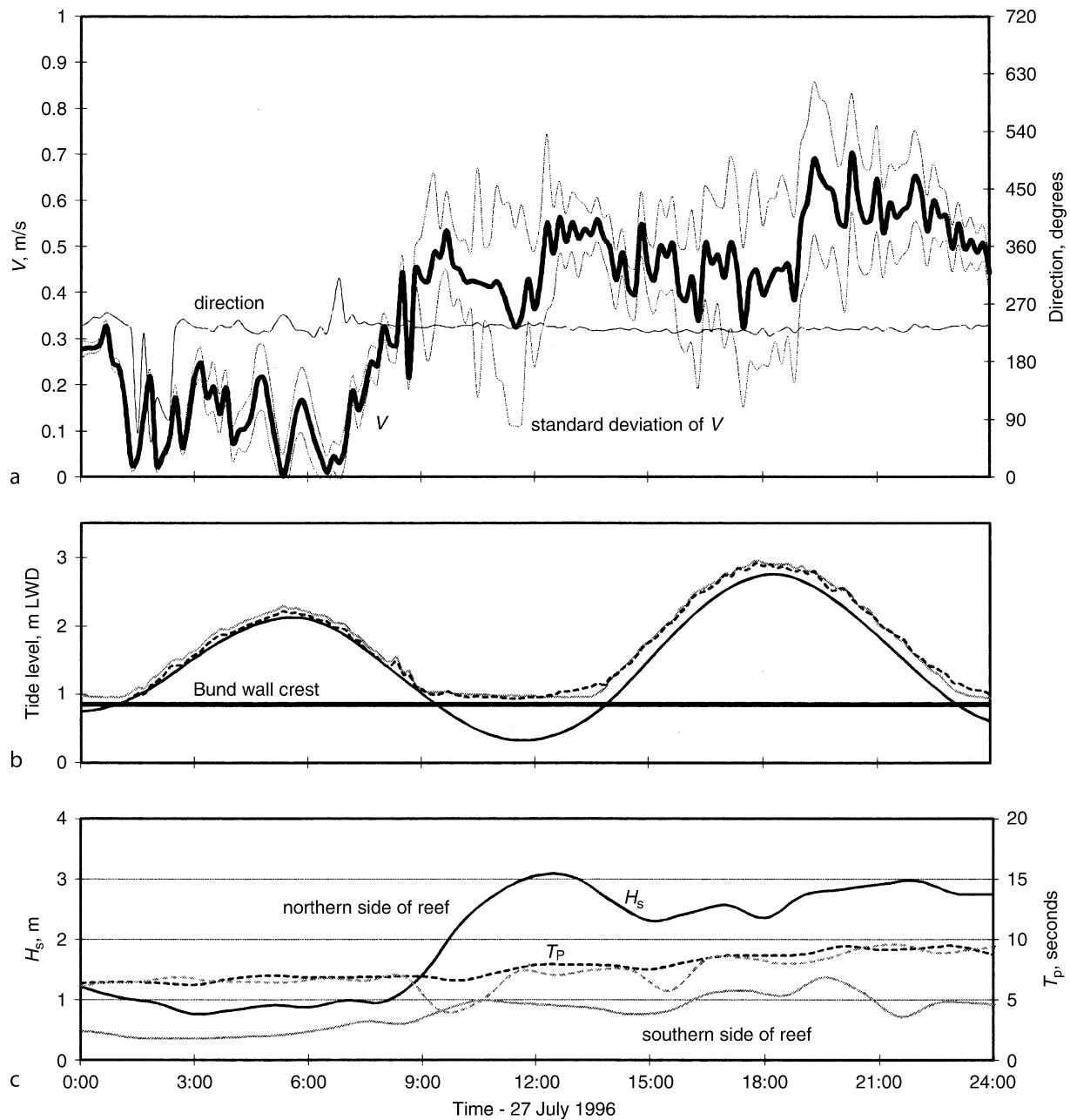
### Summary

Knowledge of ocean waves comes from observation and measurements in the field, laboratory experiments, mathematical theories, and numerical models. Engineering works, modern warfare, and environmental management have all stimulated and contributed to scientific research concerning ocean waves and their influence on coral reefs.

Waves are one of the most important physical phenomena shaping the morphology and influencing the ecology of modern coral reefs and reef top islands. There is a large spectrum of ocean waves, ranging from wind waves, swell, tides, storm surges to tsunamis. This entry is concerned with wind waves and swell.

Small amplitude wave theory is a first order linear theory for oscillatory waves of sinusoidal form. It provides





**Waves and Wave-Driven Currents, Figure 14** Wave-driven currents dominate over tidal currents at Heron Reef, southern GBR – 27 July, 1996 (adapted from Gourlay and Hacker, 2008b, p. 179).

relationships between the wave length, wave period, wave celerity, and wave height as waves propagate from deep water, where waves are unaffected by the bottom, through intermediate depths, where the depth has an increasing effect, into shallow water, where the depth dominates the propagation of the waves (see also Chapter *Wave Shoaling and Refraction*). As waves propagate across the water surface, water particles disturbed by them move in closed orbits with negligible forward transport but energy is transmitted by the waves with a velocity less than the wave celerity.

Finite amplitude wave theories give a better representation of the form of real waves, that is, the peaks are sharper and the troughs are flatter than those of sinusoidal waves. Stokes theory applies for deep water waves, and the second order theory predicts a small net movement of water particles or mass transport in the direction of wave propagation. Cnoidal wave theory represents shallow water finite amplitude waves.

Waves break when their crests become unstable. In deep water this appears as white caps at the front of the

wave crests. In shallow water there are a series of breaker forms, spilling, plunging, collapsing, and surging, depending upon the steepnesses of both the bottom and the waves. The region between the break point and the shore is known as the surf zone, the final section of which is the swash zone on the beach face.

Real ocean waves are not periodic but irregular. The characteristics of real waves measured by a wave recorder are represented by the significant wave height or root mean square wave height, which are related to one another by the Rayleigh distribution. An alternative or complementary representation of irregular waves is the wave spectrum that measures amount of energy at different frequencies in a given short-term wave record.

The interaction of physical processes on coral reefs is complex, and wave transformation occurs in water depths that are constantly changing with the tides in different locations with varied reef morphology. The types of waves propagating on reefs include sea and swell from the surrounding ocean, short locally generated wind waves, secondary waves, and infragravity waves. Waves are affected by the rough reef face before breaking on the reef rim, after which they reform and travel across the reef flat and ultimately may break on the beach of a cay or other land mass. For any given water depth over a reef there will be a limiting wave height that can cross the reef without breaking. Both field and laboratory experiments indicate that the significant wave height of reformed waves on a reef does not exceed 0.35–0.4 times the water depth on the reef, and the maximum individual wave height is no more than 0.55–0.6 times the water depth. Reef surfaces are 10–20 times rougher than sandy beaches, and 72–97% of wave energy is dissipated as waves propagate across reefs. High and wide reefs dissipate much more energy than low and narrow reefs. Winds and the waves they generate vary seasonally, and these variations have significant implications for the formation, shape, and location of reef islands on individual reefs.

*Wave Set-Up* causes variations in mean water level on reefs, and the resulting water level gradients drive reef top current systems. Wave-driven currents flow from the exposed reef edge, where waves are breaking, toward the sheltered side of the reef and/or to lower parts of the reef top or atoll reef. Outflowing currents through both natural and artificial channels have the potential to remove sediment from the reef.

Mathematical models of wave-driven currents are based upon the depth-integrated equations of motion for steady free surface flow, that is, momentum equation incorporating wave thrust, and continuity equation. These models predict that the wave-driven flow over a reef increases from zero, as the ocean water level rises above the reef top level, to a maximum with increasing water depth and then decreases as wave breaking and wave set-up reduce, becoming zero again when waves pass over the reef without breaking. Such models also can simulate wave-driven circulation in the presence of tidal circulation. However, they are restricted to reefs with relatively flat reef face slopes and generally

do not produce meaningful results when water depths over the reef are very shallow.

The wave pump analogy regards the waves breaking on the reef as a pump lifting water from the ocean and discharging it onto the reef top or into the lagoon behind the reef. The pumped water then flows back over the leeward side of the reef in accordance with open channel flow theory. The wave pump can be applied to and is most efficient on steeper faced reefs. It can also be applied where reef top water levels are very shallow or even emergent, that is, above ocean water level. Reef top characteristic curves for a given reef show the increase in wave-driven flow from zero at very small depths to a maximum at much larger depths and then decreasing to zero when waves pass over the reef without breaking. They also show the different flow conditions when reef top control and reef rim control occur and the critical submergence when one form of control changes to the other. Field measurements show that wave pumping provides a very effective mechanism for flushing atoll lagoons, particularly those that are completely enclosed by a reef with no channels through its rim.

In open ocean situations, even when tides are relatively large (range  $\leq 3$  m), wave-driven currents significantly influence the reef top circulation system on platform reefs. On a particular reef, under commonly occurring wave (1.5 m height) and tidal conditions, the incoming tidal flow was completely reversed by wave-driven flow even though the maximum wave-driven currents on the reef top were usually no larger than 0.3–0.4 m/s. However, during storm events with ocean waves  $\leq 3$  m height, currents were at least 0.6 m/s. When tidal currents were insignificant, the wave pump theory gave a good prediction of reef top current velocities.

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## Cross-references

Cay Formation

Engineering On Coral Reefs With Emphasis On Pacific Reefs

Fringing Reef Circulation

Hydrodynamics of Coral Reef Systems



Infrastructure and Reef Islands  
 Lagoon Circulation  
 Reef Front Wave Energy  
 Spurs and Grooves  
 Tidal Effects on Coral Reefs  
 Tropical Cyclone/Hurricane  
 Tsunami  
 Wave Set-Up  
 Wave Shoaling and Refraction

## WEST INDIAN CORAL REEF CLASSIFICATION

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### Definition

Coral reef classification: Assignments of single coral reefs or of parts thereof to reef types distinguished by their zonal structure. The present reef classification is ecological and based on the occurrence and distribution of certain coral associations (“facies zones”) that develop as a result of differential exposure to waves.

### Introduction

As a side result of his longtime taxonomic studies in the northern Red Sea, Benjamin Klunzinger (1870) described for the first time in great detail the zonal distribution of reef biota parallel to the front of a fringing reef. Almost 85 years later, a well-developed zonal pattern was reported again by Wells (1954) from Bikini atoll in the western Indo-Pacific Ocean. Wells (1954, 396) defined the “ecological zone” of a coral reef as “an area where local ecological differences are reflected in the species association and signalized by one or more dominant species”. Thus, distribution of reef builders is essentially controlled by “ecological differences” (primary environmental factors) such as substratum (soft or hard), water depth (diminution of luminosity with increasing depth), wave exposure and intensity of seasonal abrasion. All of these fore-mentioned factors are entirely physical in nature (Geister, 1975, 1980a).

From Jamaican reefs, Goreau (1959) presented a first detailed description of coral zonation in the western Caribbean Reefs region. Studying southwestern Caribbean reefs, Geister (1975) analyzed zonal patterns of the reef complex surrounding San Andrés Island, the reef zones being interpreted as facies units. The nature and causes of this and other benthic zonations, found both in Caribbean Reefs and Indo-Pacific reefs, were reviewed by Done (1983).

### Composite structure of shallow Caribbean coral reef types

The monograph of Geister (1975) provided a first attempt of an ecological classification of shallow West Indian reefs

based on the eye-catching zonal pattern of the frame-building biota (facies zones) corresponding to graduated exposure to waves.

Waves in the West Indies are essentially generated by the trade winds blowing with rather constant force from easterly directions. When incoming waves approach over the fore-reef slope of coral reefs, a gradual increase of bottom water movements is observed as an effect of shallowing. Maximum water movement is observed in the reef crest area where waves normally break (“breaker zone”). Decreasing hydrodynamic energy on the bottom behind the topographic crest is due to energy loss by wave friction and by the effect of gradual deepening.

Graduated wave exposure on ridge-shaped coral reefs is mirrored by striking sub-parallel facies belts of the reef building biota (Figure 1). These are both ecological and facies zones defined by dense growths of predominant hermatypic corals, mixed coral associations or other reef biota adapted to different degrees of wave exposure.

The wave zones recognized in Caribbean reefs are listed below, following a sequence of decreasing wave exposure:

- (1) **Melobesieae wave zone** (“algal ridge”)
 

Red algae forming massive algal encrustations
- (2) ***Palythoa-Millepora* wave zone**

*Millepora* spp. framework associated with the colonial zoanthid *Palythoa* sp.
- (3) ***strigosa-palmata* wave zone**

*Diploria strigosa* heads with *Acropora palmata* thickets
- (4) ***cervicornis* wave zone**

*Acropora cervicornis* thickets, almost monospecific
- (5) ***porites* wave zone**

*Porites porites* thickets, almost monospecific
- (6) ***annularis* wave zone**

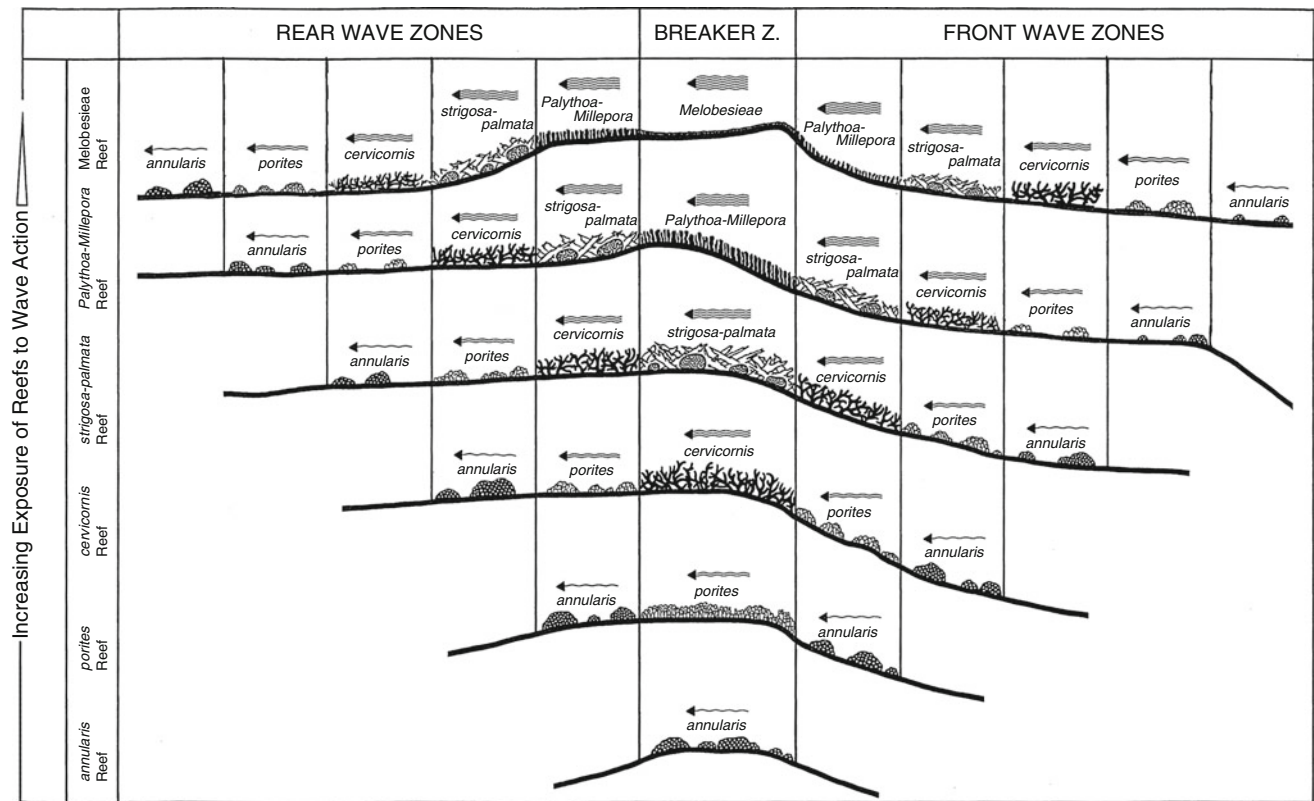
*Montastrea annularis* (and related species *M. franksi* and *M. faveolata*) massive heads in mixed faunal complex including some branching species.

Where well-developed, an overall symmetrical arrangement of subparallel “wave zones” will be recognized from the fore-reef (“front wave zones”) to the back-reef area (“rear wave zones”). This composite zonal structure is best developed in crest-shaped subtidal reefs facing the incoming waves (Figure 1). It permits to define six basic reef types. Each reef type is recognized by and named after the wave zone community on the reef crest (“breaker zone community”). This breaker zone community reflects the maximum wave exposure characteristic for each reef.

We distinguish the following six basic “reef types” (Figure 1) arranged according to decreasing wave exposure:

Melobesieae reef > *Palythoa-Millepora* reef > *strigosa-palmata* reef > *cervicornis* reef > *porites* reef > *annularis* reef

Sequences of wave zones in front and to the rear of the breaker zone (reef crest) reflect successively more sheltered conditions on the sea bottom. If well developed, their



**West Indian Coral Reef Classification, Figure 1** Idealized complete zonal sequences of the six basic reef types present in West Indian reef complexes. Increase in relative degree of wave exposure is indicated by simple to multiple arrows. The uppermost profile represents a reef exposed to maximum wave energy, the lowest to a minimum. The scheme shows a successive dropping out of high-energy associations with decreasing wave exposure and a shift of deeper water associations to shallower locations on sheltered reefs. Zonal sequences are normally incomplete, commonly with zonation gaps in the fore-reef and back-reef areas. Modified from Geister (1983).

zonal sequence may be rather complete as shown in Figure 1. But more frequently, parts of the front and rear wave zones are missing leaving empty zonal gaps.

Incomplete or irregular series of wave zones result from irregular bottom topography in front or rear of the crest, from steep break-offs, unusually shallow reef flats, substrate changes from reef to lagoon facies (unsuitable substratum of loose sediments for settling corals!) and from rocky surfaces exposed to extreme seasonal storm waves causing abrasion (see Geister, 1977: Figure 1). The distribution of these six basic reef types within the reef complex of San Andrés Island was presented in a map (Geister, 1975: Figure 23).

Comparable studies in the Indian Ocean (Rosen, 1975) suggest that the same principles of wave zonation are effective both in Caribbean Reefs and Indo-Pacific coral reefs. Exact comparison, however, is necessarily bound to reefs of the same faunal realm.

### Regional and local distribution of reef types

Reef classification based on ecological zonation facilitates comparative studies of regional reef distribution and reef mapping at scales ranging from single small patch reefs up

to large reef complexes. Thus, a follow-up study (Geister, 1977a) analyzed the geographic range of these reef types over the entire West Indian faunal province. Regional distribution of reef types mainly concerns seaward reefs around oceanic islands, atolls, and in front of continental coasts but also fringing and patch reefs within the lagoons of barrier reefs and atolls (Geister, 1975, 1977a, 1983, 1992; Geister and Diaz, 1997; Diaz et al., 2000; Geister and Diaz, 2007).

Reefs of **extreme wave exposure** (Melobesiaee reefs) are regionally restricted to areas facing a maximum windward fetch of the trade winds reaching up to 2,000 or more kilometers in length. Thus, these reefs are best developed along the eastern shores of the Lesser Antilles (Adey and Burke, 1976), where they receive the full impact of the Caribbean Reefs swell. Melobesiaee reefs at the western ends of the Caribbean Sea and Gulf of Mexico are restricted to particular local topographic conditions where wave refraction and interference enhance local wave intensity (San Andrés Island, Providencia, San Blas/Panama, etc.).

Reefs of **high wave exposure** are those of the *Palythoa-Millepora* type. They are best developed in the unprotected windward tracts of the central Caribbean (Pedro Bank etc.) and in the atolls and island barrier

reefs along the Nicaraguan Rise and western Gulf of Mexico where the fetch of the trade winds attains around 500–2,000 km in length.

Seaward reefs of the *strigosa-palmata* type reflect **medium wave exposure**. They are found protected from the full impact of oceanic swell by a wide shelf area or land mass as in Jamaica (Goreau, 1959), or lie in leeward positions facing a continental coast (Caribbean coast of Colombia: Diaz et al., 2000). They also flourish in the wave shade of higher wave exposure reef complexes as at Belize or in the lagoons of barrier reefs and atolls.

Reef types reflecting **moderate** (*Acropora cervicornis*), **low** (*Porites porites*) and **minimum wave exposure** (*Montastrea annularis*) are mainly bound to protected lagoonal environments of major reef complexes. In addition, they flourish in the quieter waters of the lagoon floor at several meters of water depth (see Geister, 1975: Figure 23; Geister, 1992; Wallace, and Schafersman, 1977; Diaz et al., 1997). Where protected from oceanic swells, they may also characterize well-sheltered leeward sectors of atoll reefs, as at Belize.

Local variation in distribution patterns of reef types can best be observed within the lagoons of single atoll or barrier reef complexes (Geister, 1975; Wallace, and Schafersman, 1977; Diaz et al., 1997). There, patch reefs will be found distributed corresponding to the local wave exposure pattern (see Geister, 1975: Figures 6 and 23).

### Lateral transitions along a single reef tract from one to another reef type

Along a same seaward reef tract, wave exposure will decrease from exposed windward towards more protected leeward positions. It will also decrease at locations where the reef crest is submerged for several meters, or where diffraction of swell occurs. Hence, single seaward reef tracts of barriers or atolls may reveal zonation patterns of more than one reef type as here defined.

### Vertical transitions in time from one to another reef type and sea-level history

The three-dimensional zonal structure of modern reefs records Holocene sea-level history (Geister, 1983: Figures 49–54). This is exemplified by a standard reef composed of the following three wave zones: *M. annularis*, *A. cervicornis* and *A. palmata* that developed under conditions of stable, slowly rising, rapidly rising and falling sea level. Intermediate situations are common:

#### Horizontal zonation pattern (Type A)

As soon as a fairly stable sea level position was achieved for some extended period after the Holocene transgression, reef growth resulted in an essentially horizontal pattern of internal zonation: lateral growth widened the established facies zones. Growing vertically into higher energy levels, they were succeeded by the wave zone corresponding to the next higher energy level. Thus, vertical transitions from an *annularis* Reef, to a *cervicornis*

Reef and finally to a *strigosa-palmata* Reef are possible (Geister, 1983: Figure 49, 50).

#### Vertical zonation pattern (Type B)

As soon as renewed sea level rise equaled the rate of reef growth, a pattern of vertical parallel facies zones developed from a Type A reef into an overall U-shaped zonal structure. The facies zone of highest wave exposure is found in the center, and successively lower wave exposure facies will grow towards the outer margins of the reef body (Geister, 1983: Figure 51). This geometry corresponds to the “keep-up reef” of Neumann and Macintyre (1985).

#### Lens-shaped zonation pattern (Type C)

When sea level rise eventually surpassed the growth rate of the Type A reef, the latter was gradually enveloped by facies zones of successively lower hydrodynamic energy, thus resembling an onion peel structure (Geister, 1983: Figure 53). Characteristic for this reef type is an upward sequence of facies zones, which reflects decreasing wave exposure and final reef drowning (Blanchon and Shaw, 1995). Breaker zones are covered by facies of successively lower wave exposure. This geometry corresponds to the “give-up reef” of Neumann and Macintyre (1985).

#### Cap-on-cap zonation pattern (Type D)

The internal facies geometry of a reef growing during a period of relative sea level lowering is characterized by a cap-on-cap arrangement of facies zones indicating downward increase of wave exposure with time. It may eventually lead to the emergence of the crest as a rocky reef islet. The best modern examples from the Caribbean Sea are the emerging reefs of the Rosario Islands chain and neighboring Baru Peninsula in Colombia (Geister, 1983: Figure 54; Pl. 26/4).

### Occurrence and distribution of reef types in the Pleistocene of the West Indies

Of the six reef types defined herein for the modern Caribbean Sea, five were found in Late Pleistocene (mostly Sangamonian) reefs of the West Indies. Thus, modern reef types may also serve as models for comparative palaeoecological studies and for mapping of Pleistocene reef tracts (Geister, 1975: Figure 27; Geister, 1980b).

However, during a preliminary survey comprising the emergent reefs of the whole West Indian faunal province, no reefs corresponding to the *Palythoa-Millepora* type were encountered (Geister, 1980b). The reason may be that the fire coral *Millepora* was rare at that time and locally absent from Sangamonian reefs.

On the other hand, the *annularis* to *porites* wave zones in Sangamonian backreefs were locally dominated by extensive thickets of *Pocillopora* sp., a branching reef coral genus completely absent from modern West Indian reefs (Geister, 1977b, 1984: Figures 13 and 14).



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## Cross-references

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## WESTERN ATLANTIC/CARIBBEAN, CORAL REEFS

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## Definition and introduction

Scleractinian corals occur all throughout the western Atlantic; however, reefs are only formed in a belt between 32.3°N (Bermuda) and ~17.5°S (Brazil). The continuous reef belt occurs between 26.5°N (Florida) and 9.8°N (Colombia) with an isolated southern extension in Brazil, separated from the Caribbean reef belt by the Orinoco and Amazonas rivers, and Bermuda as an outlier to the north. The western Atlantic forms its own biogeographic province and harbors a unique coral fauna that diversified primarily after the closure of the Isthmus of Panama, but the evolution of which may have already begun in the Eocene. All reef types known from other reef areas also occur in the western Atlantic, but some reef types are unique.

## The coral fauna

The Caribbean/western Atlantic region is home to a unique coral reef fauna and therefore makes up a distinct biogeographic province. Within this province subtle difference further subdivides it into a Bermudian (lacking *Acropora*), northern (E-Florida/Bahamas), north-western (Gulf of Mexico, W-Florida), central (Mesoamerica, Antilles), and Brazilian subregion (Veron, 1995). The most distinct region is the Brazilian with several endemic species and an endemic genus (*Mussismilia braziliensis*, *M. hispida*, *M. hartii*, *Favia gravida*, *F. leptophylla*, *Siderastrea stellata*, *Millepora braziliensis*, *M. nitida*, *M. laboreli*; Leao et al., 2003; Amaral et al., 2008). The Brazilian fauna has

affinities to the Tethyan and Paratethyan Miocene faunas, where these genera were common (Leao and Kikuchi, 2005).

Within the Atlantic Ocean, only the western region supports coral reefs. The easternmost Atlantic harbors corals, but no true reef building, although some dense coral growth is reported from the Gulf of Guinea and the Cape Verde Islands (Laborel, 1974; Moses et al., 2003). The Mediterranean, up to the Miocene a locus of vigorous coral growth, has been essentially devoid of any reefal development since the Messinian Salinity Crisis, during which the Mediterranean desiccated or at least became hypersaline (Brachert et al., 1996). It later refilled with cryospheric Atlantic middle water, thus displacing its warm water fauna with one of cold water, that has never been fully displaced even though the Mediterranean has warmed since. In the Plio and Pleistocene, and in some places also in the Holocene, *Cladocora caespitosa* formed sizeable (meters thick) banks (Aguirre and Jimenez, 1998). Algal-built hardgrounds (the coralligène, Bosence, 1985a) and *Cladocora* banks presently occur, but are at best analogues to more ancient, but not equivalent to recent W-Atlantic reefs.

The end-Miocene, early Pliocene faunal crisis in the eastern Atlantic left an isolated but highly diverse fauna with mainly Indo-Pacific species in the western Atlantic that was fully isolated with the formation of the Panamanian land bridge in the lower Pliocene (~3.5 Ma = million years ago; Collins et al., 1996). During the period of 6–1 Ma, the Indo-Pacific fauna was progressively reduced by a relatively slow step-down extinction and replaced by pulses of modern Caribbean fauna. Seventeen of 41 genera living in the Caribbean in the Pliocene became extinct, 11 of these genera continued to exist in the Indo-Pacific. No new genera originated and, with the exception of *Pocillopora* which disappeared again, no species immigrated (Budd and Wallace, 2008). Prior to this turnover, shallow areas were dominated by *Stylophora* and *Pocillopora*. One of the most iconic species of the Caribbean coral fauna, *Acropora palmata*, is first reported from Costa Rica (Quebrada Chocolate Formation) about 3.6–2.6 Ma (McNeill et al., 1997). *A. palmata* was rare at the beginning of its rise. *A. cervicornis*, however, commonly cooccurred with *Stylophora* in several late Pliocene formations (e.g., in Costa Rica, Jamaica, and Curaçao; Budd and Wallace, 2008). Several other *Acropora* (two of the subgenus *Isopora* which presently only occurs in the Indo-Pacific) had existed in the Caribbean but had all disappeared during the last extinction pulse around 2 Ma. Molecular analyses have shown that several traditional families of coral may be polyphyletic (e.g., Faviidae, Mussidae), and may be even many genera (e.g., *Montastraea*, *Favia*, *Scolymia*). A distinct clade in Atlantic members of the Faviidae and Mussidae suggests that the relationship between Atlantic and Indo-Pacific corals may indeed not be very close and divergence could predate final closure of the Central American Isthmus in the Pliocene to as early as the Eocene. Nine of the 27

genera of reef-building Atlantic corals belong to this previously unrecognized lineage, which probably diverged over 34 Ma (Fukami et al., 2004) (Figure 1).

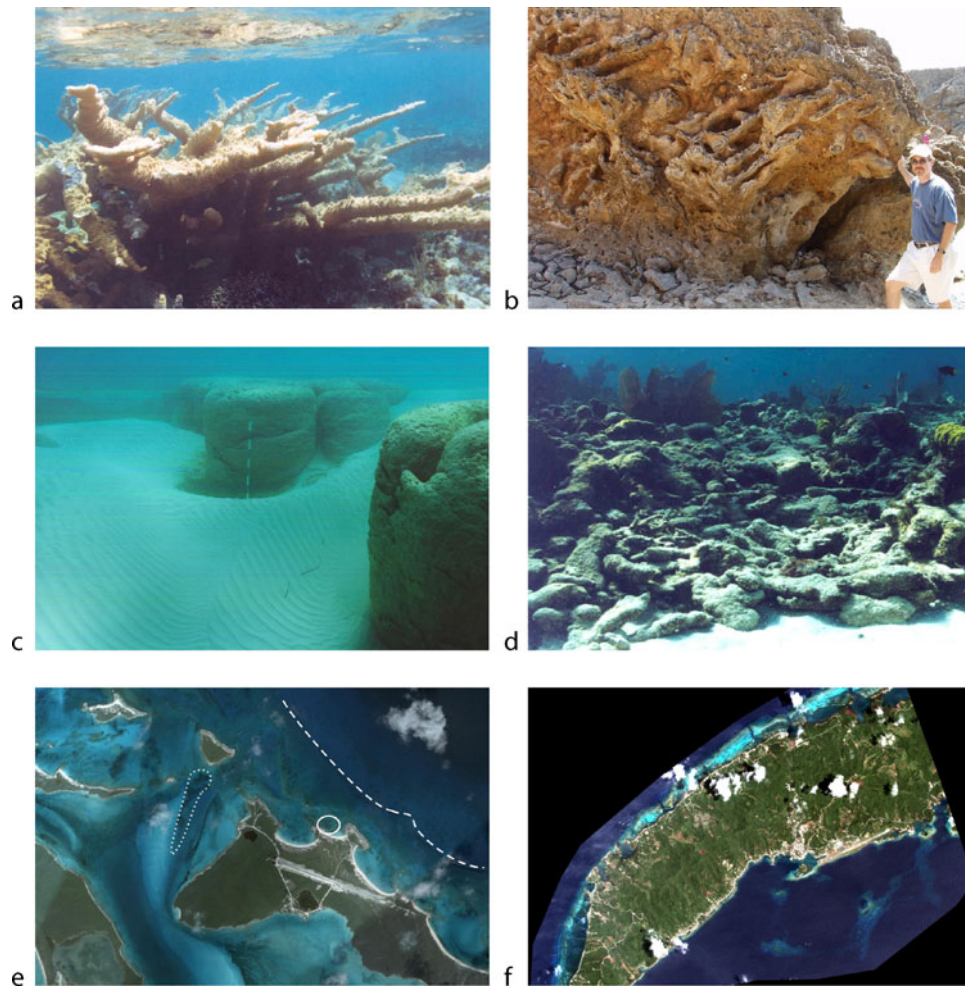
### Loss of long-term ecological stability

Remarkable ecological stability has been observed in Caribbean coral assemblages throughout the Pleistocene and Caribbean coral reefs exhibit a clear zonation pattern throughout the region (Geister, 1983). It has been shown that coral community structure on Caribbean coral reefs reassembled after global sea-level changes in similar ways throughout a 500-ka interval (Pandolfi and Jackson, 2006). Six common coral species (*A. palmata*, *A. cervicornis*, three *Montastraea*, and *Diploria strigosa*) dominated the reef-building episodes. While not unique to the Caribbean, this is the longest demonstrated such interval of community stability. Similarly, Pleistocene community recurrence patterns were found in New Guinea (Huon Peninsula) over 115 ka (Pandolfi, 1996). In the Holocene, community stability has been demonstrated in the Caribbean (Aronson et al., 2004) and Brazil (Leao and Kikuchi, 2005). However, in stark contradiction to the situation in the Pacific, this persistence of community structure has recently been lost throughout most of the Caribbean by the almost region-wide demise of the *A. palmata* zone and equally dramatic reduction of *A. cervicornis* (Pandolfi and Jackson, 2006). Also in Brazil, community patterns and coral density that have shown relative stability on millennial scales have recently changed (Leao and Kikuchi, 2005).

### Types of reefs and frameworks

The W-Atlantic/Caribbean region exhibits reef growth in all the classic carbonate sedimentological settings (Schlager, 2005; Hine et al., 2008): ramp (W-Florida, NE Yucatan), unrimmed shelf (Yucatan, Brazil), attached rimmed shelf (SE Florida and Florida Keys, Cuba, Belize), and rimmed shelves on unattached (or isolated) platforms (Bahamas banks, Chinchorro, Belize banks, etc.). A specialty of Atlantic rimmed shelves is coral reefs often cooccurring and alternating with grainstone shoals (frequently ooids, i.e., Bahamas and Yucatan).

In the shallowest regions of the shelf, typical *fringing reefs* (e.g., around St. Croix, Vieques, Lesser Antilles, Cayman Islands, Jamaica, Roatan, etc.) or *bank-barrier reefs* (such as developed in the Florida Keys or the SE Puerto Rico shelf) occur. Many of these fringing reefs are built by *A. palmata* frameworks in situ, although some are not and consist mainly of rubble (see below). Many such structures initiated about 8–6 ka and either continued growing until today or, as in the high-latitude SE Florida continental reef tract, experienced a switch off around 6–4 ka. On the middle shelf, *mid-shelf reefs*, situated at a depth level intermediate between shelf-edge and fringing reefs, are reported from many Caribbean localities (Puerto Rico, Vieques, Florida, Cayman, etc.). Blanchon et al. (1997) explained mid-shelf reefs at Cayman as a result of stepped Holocene sea-level change, i.e., periods



**Western Atlantic/Caribbean, Coral Reefs, Figure 1** (a) *Acropora palmata*, an iconic species for the Caribbean coral fauna (here at Lee Stocking island, Bahamas), has recently experienced significant die-back throughout its range (b) long-term ecological stability throughout the Pleistocene (outcrop in Curacao), (c) stromatolites can form small fringing reefs in the Bahamas or subtidal structures, such as these at Lee Stocking island, Bahamas. Measuring stick = 1 m. The stromatolite with the stick shows artichoke-like leaves, (d) rubble is an important constituent of Caribbean reef frameworks and now all that is left of the former *A. palmata* zone throughout much of its range, (e) islands on the northern Caribbean banks do not have fringing reefs. Shown is Lee Stocking Island on the Great Bahama Bank, the only area of shallow *A. palmata* reef is shown in a circle, the area of subtidal stromatolites within a dotted polygon, and the trend of the mid-shelf reef (at about 10 m depth) with a dashed line. (f) The western end of Roatan (Bay Islands, Honduras) with a typical fringing reef and three offshore bank reefs to the south.

of unusually rapid and then slowing sea-level rise. The realism of this sea-level assumption (as that of many others) is, however, being debated (Hubbard et al., 2008; Blanchon et al., 2009) and mid-shelf structures can be found at variable depth and with variable morphology (Banks et al., 2007; Hubbard et al., 2008), making their explanation purely by sea-level difficult since antecedent topography may have also played a role. *Shelf-edge reefs* are a typical feature throughout the Caribbean and have been described in detail from Barbados (Macintyre, 1988), Florida (Lighty et al., 1978, Banks et al., 2007), St. Croix, the Lang Bank, and Puerto Rico (Hubbard et al., 1990, 2008). They are typically built by *A. palmata*, are situated at depths around 20 m, initiated around

12–10 ka, and flourished until ~8 ka. Tracking rising sea level, they then stepped back throughout the Caribbean to form the wide variety of shallower shelf reefs. In Belize and Mexico, the Caribbean also has one of the world's biggest *barrier reefs*, a largely structurally controlled feature where reef development is guided and determined by fault lines (Purdy et al., 2003), lowstand karst topography (Purdy, 1974), and paleo-river beds (Esker et al., 1998). Other large barrier reefs exist in the Bahamas at Andros, in the Turks and Caicos, Venezuelan off-shore banks, etc.

Deep, submerged *bank reefs* occur in the Gulf of Mexico (half a dozen banks of which the Flowergarden banks are the most famous, Schmahl et al., 2008), where they are associated with salt diapirism, on the Nicaragua rise, and



in Brazil (Leao et al., 2003), where they often consist of bedrock (older limestones or crystalline basement). Unusual, bank-like, deep reefs also occur off SW-Florida, such as the carbonate banks of the Florida Middle Grounds and a drowned dune/coastal spit complex at Pulley ridge (Jarrett et al., 2005). These deep banks are home to unique, and frequently dense, coral assemblages (Hine et al., 2008).

Several reef types unique to specific Atlantic region exist. *Outlier reefs* in the Florida Keys Reef Tract (Lidz et al., 2008; Hine et al., 2008) are Pleistocene reefs situated on an upper-slope terrace, separated from the present shelf edge with its shelf-edge reefs by a well-developed trough. Outlier reefs form a discontinuous and drowned (surfaces at around 10 m below MSL), largely parallel tract to the major present reef trend on the shelf edge. The outliers comprise a stacked sequence of reefs from MIS 5c at the base to 5b and 5a at the contact to Holocene overgrowth and Lidz et al. (2008) consider them testament to optimal platform margin settings for reef growth during 5c and later times. *Algal cup reefs* occur in Bermuda. They are somewhat reminiscent of the Brazilian Chapeiros (mentioned below) inasmuch as the cup reefs can also take a mushroom-shaped appearance. The tops are made by calcareous algae and can have a raised rim and a slightly deeper interior. They are mostly built by calcareous algae, the gastropod *Dendropoma irregulare* and *Millepora* spp. (Ginsburg and Schroeder, 1973). *Algal ridges* occur throughout the Lesser Antilles that are built by several thousand years of algal growth (Adey and Burke, 1976) and off Cozumel, *coralline algal microatolls* occur (Boyd et al., 1963). *Chapeiros* in Brazil are pinnacle reefs made of Holocene reef limestone that consist of isolated narrow pillars that expand on the top to take a mushroom-shaped appearance (Leao et al., 2003). These reefs can be 5–25 m high and have diameters of 5–50 m at their tops and are mainly built by coral. This type of reef is restricted to the Abrolhos reef complex in southern Bahia State, where a wide variety of morphologies of isolated and coalescent Chapeiros exist. On many other Brazilian reefs, most particularly close inshore, substratum for coral growth is frequently on the former beachrock, indurated dunes, or bedrock (igneous or carbonate). This situation is reminiscent of high-latitude reefs in the Indo-Pacific, with corals in SE Africa and SE Australia carpeting indurated sand dunes and beachrock ridges. *Stromatolites* are microbialites that are common and attain large sizes along the Exuma margin in the Bahamas. Modern stromatolites, which are layered sedimentary rocks formed by sediment-trapping microbial mats, are rare and best documented from W-Australia (Shark Bay) and the Bahamas (Reid et al., 1995). The Bahamian stromatolites can be domal, molar shaped, or elongate and have some leaf-shaped structures that are reminiscent of Precambrian stromatolites. At Stocking Island and Highbourne Cay in the Bahamas, regular small fringing reefs are dominated in their backreef areas by stromatolites and toward the beach by thrombolites (Macintyre et al., 1996; Reid et al., 1999; Andres et al., 2009). These stromatolites are <1 ka of age and grow on a Holocene reef that was killed by sediment trapping in the lagoon after the emergence of

the reef edge, built by coralline algae. These Bahamian stromatolite reefs are unique, their only known Pacific counterparts in Shark Bay (Playford and Cockbain, 1976) or in Tikehau lagoon (Sprachta et al., 2001). The latter, however, occur in a high-nutrient setting, while the Bahamian stromatolites occur in nutrient-poor setting.

In deep water, off Florida, the Bahamas and in the Gulf of Mexico, well-developed *Lithohierms* occur (Neumann et al., 1977; Roberts, 1992). These are defined as deep-water mounds formed by successive episodes of submarine lithification of sediment which may contain carbonate skeletal debris and are often locus of tropical reefal assemblages (Messing et al., 2008). In the Gulf of Mexico, many consist of authigenic carbonates precipitated in conjunction with bacterial utilization of hydrocarbon gases and crude oil produces (Roberts, 1992). Also, *deep-water reefs*, built among others by the corals *Lophelia pertusa*, *Oculina varicosa*, and *Madrepora oculata*, can form significant three-dimensional carbonate buildups in Florida, the Bahamas, and the Gulf of Mexico (Messing et al., 2008).

### Similarities and differences to Indo-Pacific reefs

While the same nomenclature is used for reefs in the Caribbean/western Atlantic, there can be marked differences in the structures of reefs between the two regions. While in both oceans shallow reef zones are characteristically dominated by the genus *Acropora*, the difference in growth form between Atlantic and Indo-Pacific members of this genus causes differences in the structure of frameworks. Caribbean reefs built by *A. palmata* can differ from those of the Indo-Pacific by consisting of more or less dense stands of *Acropora* trunks that get filled in by debris (usually broken *A. palmata* branches) later to get cemented. Hubbard et al. (1998) described Caribbean reefs as “more a garbage pile than an in place assemblage of corals cemented together in a rigid framework,” as is more usually observed in the Indo-Pacific (Hopley et al., 2007). Indeed, some Caribbean reefs are largely devoid of reef builders in situ and consist almost exclusively of tossed debris, without much living veneer (e.g., the Grand Cayman fringing reef; Blanchon et al., 1997; sections of the Vieques fringing reef, Rasser and Riegl, 2002). It appears that rubble binding by red algae and sponges is more efficient in the Atlantic than in the Indo-Pacific (Rasser and Riegl, 2002). The importance of coral facies (branching vs. massive) is discussed by Gischler (2008) and Hubbard et al. (2008) – interestingly, massive facies appear to have accreted almost as rapidly as the branching *Acropora palmata* facies.

Neither the Florida Keys nor any of the islands on the major banks (Great and Little Bahama Banks, Caicos Bank, Turks Bank) are surrounded by well-cemented and continuous fringing reefs that are so typical for many Indo-Pacific atolls and carbonate banks (such as the Great Barrier Reef, island on the Red Sea banks, Maldives and Chagos banks, etc.) and are also well developed in the southern and eastern Caribbean (Bay Islands, ABC

islands). The relatively high-latitude setting of the northern Caribbean carbonate banks (Florida, Bahamas) puts them under the influence of N-American weather systems, most particularly, cold fronts (Roberts et al., 1982). Thus, alternations of strong heating in summer and strong episodic cooling of the shallow bank waters affect reef growth. On the banks, reef growth is therefore concentrated where islands shelter the reefs from the direct influence of bank waters (Ginsburg and Shinn, 1994). This is not observed on many of the banks in the more tropical Caribbean (Grovers, Lighthouse Turneffe, Chinchorro) that are indeed surrounded by luxurious reef growth.

Unique reef-like accumulations of branching corals (*Porites divaricata*) and branching algae (*Neogoniolithum strictum*) occur around Rodriguez and Tavernier Key off Key Largo in Florida (Turnel and Swanson, 1976; Bosence, 1985b). The windward edges of these banks are good examples of constratal reef building (Insalaco, 1998) inasmuch as the corals and algae form a loose framework that gets filled by muddy sediment. Although indicated by the mounding morphology, the presence of this framework is visible primarily in core but not at the sediment surface, other than by a localized higher density of branching corals and algae.

A major difference in the Indo-Pacific is the absence of evidence for an early Holocene sea-level overshoot in the Caribbean region, although it has been demonstrated in Brazil (Leao et al., 2003; Gherardi and Bosence, 2005), and the most commonly used sea-level curves show a rapid rise ( $>5\text{--}6\text{ m/ka}$ ) until about 8–6 ka, when it slowed to about 1 m/ka while ascending to today's level (Toscano and Macintyre, 2003; Hubbard et al., 2008). Throughout the Pacific, there is clear evidence of an early-to mid-Holocene temporary sea-level highstand of about 3 m, centered at 4 ka (the Brazilian record suggests a maximum of nearly +5 m at ~5 ka, with subsequent decline to today's level; Leao et al., 2003). The overshoot (generally ascribed to earth rheology) is documented in raised reefs, raised intertidal notches, or raised intertidal benches throughout the Pacific basin. The Caribbean region does not display any unequivocal such features, but Brock et al. (2008) used morphological features of northern Florida Keys patch reefs in combination with raised beach ridges to infer such an overshoot also for the Caribbean region.

## Conclusion

- Coral reefs in the Atlantic/Caribbean differ from those in the Indo-Pacific with regard to fauna as well as aspects of reef framework formation.
- The Atlantic coral fauna began its evolution prior to the closing of the isthmus of Panama, but fully diversified only afterwards.
- Remarkable ecological continuity of Pleistocene coral community organization has recently been lost.
- Several types of reefs unique to the Atlantic/Caribbean exist (stromatolitic fringing reefs, Chapeiroes, algal cup reefs, outlier reefs).

- Fringing reef and island development on the largest Caribbean banks (Bahamas banks, Florida Keys) are frequently different than in the Indo-Pacific due to relatively high-latitude position, but more comparable within the truly tropical belt (Belize, Venezuela, etc.).
- No Holocene raised reefs known from Caribbean region, only in Brazil signs of early Holocene highstand.

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## Cross-references

Bahamas  
 Banks Island: Frasnian (Late Devonian) Reefs In Northwestern Arctic Canada  
 Barbados  
 Belize Barrier and Atoll Reefs  
 Bermuda  
 Brazil, Coral Reefs  
 Florida Keys  
 Ooids  
 Sediment Durability  
 Tethys Ocean  
 Vaughan, Thomas Wayland (1870–1952)

## WESTERN AUSTRALIAN REEFS

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## Synonyms

Reefs; Western Australia

## Definition

Wave resistant structures built primarily by coral growth.

## Introduction

Situated in the eastern Indian Ocean along the western continental margin of Australia, coral reefs extend from the tropical Kimberley coast in the north to the temperate southwest (Figure 1).

This latitudinal climatic gradient places reefs in a setting likely to become increasingly significant as a natural laboratory when predictions of global climate change are considered. The relatively small human population along several thousand kilometres of coast (44% of the Australian coastline) limits anthropogenic impacts from a largely desertic coastal hinterland bordering the continental shelf. Coral reefs include fringing reefs such as the Ningaloo Reef (at 280 km long, the world's longest fringing reef), mid-outer shelf reefs such as the Houtman Abrolhos reefs, the southernmost reefs in the Indian Ocean, and isolated reefs such as the Rowley Shoals and Scott Reef as some of the better known reefs, but there are many other poorly known and remote systems in the region.

## Regional oceanography

Three oceanographic and biogeographic provinces (Figure 1) present along Australia's west coast are: the Northern Australian Tropical Province (11–22°S), the

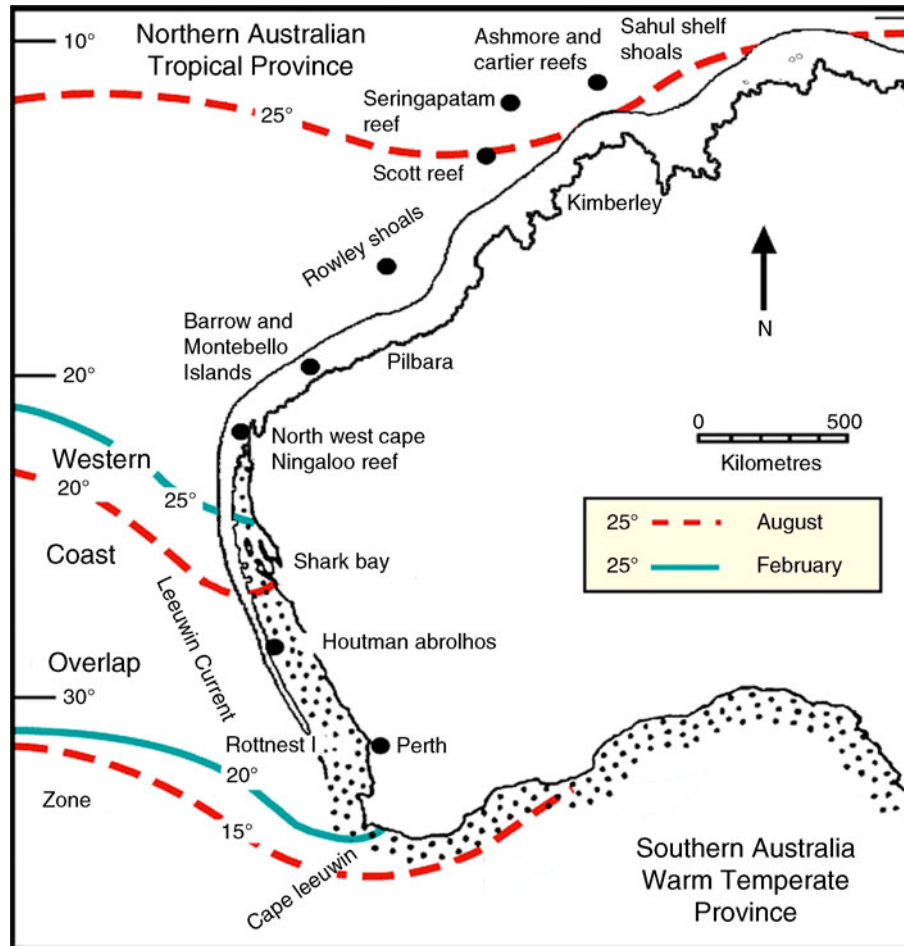
Western Coast Overlap Zone (22–32°S), and the Southern Australian Warm Temperate Province (south of 32°S). This regional oceanography is influenced by the South Equatorial Current, at 5–15°S latitude, driven by easterly trade winds, and the Indonesian Throughflow, which floods the North West Shelf with warm, low salinity water, resulting in sea levels in the tropics being 0.5 m higher than along the southern coast of Australia. With higher tropical sea levels, the formation of a north-south pressure gradient induces a weak easterly flow of central Indian Ocean subtropical water toward the Australian coast between 15–35°S (Pearce and Griffiths, 1991). This easterly flow is deflected south by the coastline, eventually contributing to the Leeuwin Current, a warm low salinity current which flows from the Indonesian Throughflow, southward along the adjacent shelf in winter. The Indonesian Throughflow delivers larvae of both Pacific and Asian reef species southward, and the Leeuwin Current is an important control on southward larval delivery, whilst suppressing upwelling (Hatcher, 1991). Tidal range and cyclone frequency decrease from north to south. The North West Shelf is cyclonic and tidally dominated, with a mean spring range from 9.2 m in King Sound to 1.7 m at Ningaloo Reef (Harris et al., 1991). Both Scott Reef and Rowley Shoals have semi-diurnal tides with a spring range of 4.5 m. At the southerly limits the coral growth reefs are microtidal (1 m) and swell wave dominated with low cyclone frequency (1 per 4 years).

## Reef morphology

Studies of Australian reefs have been dominated by work on the eastern seaboard and the Great Barrier Reef (see Hopley et al., 2007), but reefs of the western continental margin of Australia and its bordering carbonate ramps remain relatively unknown. Coral reefs of Australia's western margin include isolated oceanic atoll-like reefs (Ashmore Reef, Seringapatam and Scott Reefs, Rowley Shoals); island-associated shelf reefs and fringing reefs of the Kimberley coast and Dampier Archipelago; Pilbara reefs (Barrow and Montebello Islands); Ningaloo Reef, a fringing reef adjacent to the North West Cape, and the mid- outer shelf Houtman Abrolhos carbonate platforms and reefs (Collins et al., 1993a, b, 1997, 2009).

## Mid-outer shelf reefs: the Houtman Abrolhos

Between latitudes 28–29.5°S the open, low-gradient shelf is interrupted by a 150 km long, discontinuous rim, whose seaward margin is 8–10 km east of the shelf/slope break near the 100 m isobath. The emergent rim consists of three platforms (Pelsaert, Easter and Wallabi platforms) separated by channels up to 40 m deep. Each platform rises abruptly some 40 m above a flat shelf, and culminates as reef flats and low islands. Submerged banks lie to the north and south of the platforms along the same trend. The three platforms differ geomorphologically but a windward reef, leeward reef, and lagoon with a central platform is distinguishable in each case. Both the central



**Western Australian Reefs, Figure 1** Distribution of Western Australian Reefs. Note position of Northern Australian Tropical Province (white), Southern Australian Warm Temperate Province (dots) and Western Coast Overlap Zone.

platforms and leeward reefs are expressed as small islands of various types, whereas windward reefs are wave-swept. The central platforms are the last interglacial ones in age, whereas the windward and leeward reefs are Holocene (Eisenhauer et al., 1993; Collins et al., 1993a, b; Zhu et al., 1993). The islands generally rise only 3–5 m above sea level. Extensive ‘blue-hole’ terrains and reticulate reefs occur at the eastern parts of the platforms and Holocene sand sheets have developed in both the windward and leeward lagoons (Wyrwoll et al., 2006). Central platform islands are surfaced by dense, calcified limestones, while subparallel ridges of coral rubble characterize leeward (eastern) islands.

The Houtman Abrolhos region is located within the Western Coast Overlap Zone and biotic transition (Morgan and Wells, 1991). It is characterized by the gradual replacement of a tropical fauna in the north by a predominantly temperate fauna in the south, as reflected in a variety of shelf and reef biotic elements, including corals, macroalgae, molluscs, echinoderms and fishes. Coral faunal communities are highly diverse; 184 species and 42 genera are recorded

(Veron and Marsh, 1988). The number of genera is much higher than for other ‘high latitude’ coral reefs (e.g., the Solitary Islands; Kure Atoll; Bermuda Reefs). *Acropora*, which is missing or very rare on many ‘high latitude’ reefs is the dominant coral. Although there are substantial numbers of temperate species and Western Australian endemic species the fauna at the Houtman Abrolhos is, on the balance, essentially tropical, and is generally considered to be at the southern limit in Western Australia of the tropical biota. Forty metres of Holocene reef buildup has occurred yielding high precision reef growth and sea level records for the Holocene and the last interglacial reefs (see Eisenhauer et al., 1993; Collins et al., 1993a, b).

#### Ningaloo fringing reef

Situated close to North West Cape and Cape Range, this fringing reef complex consists of a narrow reef crest, which is emergent at low water, with well-developed spur and groove morphology present on most outer reef slopes; complex multiple developments of spur and groove are also present. The reef crest is backed by a reef flat

(usually <150 m wide), which has robust coral communities, as well as coral rubble veneers, and deep grooves flooded by sandy sediment which shallow and broaden landward. A shallow (0–4 m water depth) lagoon of a width of 1–5 km consists of rock pavements with sparse corals, and mobile sandy substrates with scattered coral communities. The lagoon shore is sandy or consists of rock pavements vegetated by macroalgae, and low cliffs and emergent platforms of the last interglacial reef limestones. Reef development is interrupted by passes and transverse channels, up to 200 m wide, which are sites for water exchange between the lagoon and the adjacent shelf. Highest coral cover and reef development occur along reef passes and in the lagoon, while the outer reef slopes do not host such rich coral communities.

Ningaloo Reef lies at the northern extremity of the Western Coast Overlap Zone. Ningaloo reef corals have strong Indo-Pacific affinities, and 54 genera and 217 species of hermatypic corals have been identified (Veron, 1995). Coral cover reaches to 40% on the swell-exposed reef front, but the outer reef slopes lack rich coral communities and coralline algae are significant. Behind the reef crest coral cover varies from 5% to 40%, with the strongest reef development in the passes and in the lagoon.

The relationship between the Holocene and the last interglacial phases of reef development is clearly shown from seismic, core data, and outcrop (Collins et al., 2002). The stratigraphic cross-section for the northern (Tantabiddi) reef is based on short cores in the lagoon and in front of the reef. These core data are consistent with cross-reef seismic lines, and indicate that Holocene reef growth recolonized the Tantabiddi Terrace (last interglacial reef) near its submerged, seaward margin, and at ca. 18 m is relatively thin (e.g., when compared to the 40 m of Holocene growth at the Houtman Abrolhos). The last interglacial reef is widespread, comprising the Tantabiddi Terrace onshore and extending beneath the lagoon of the contemporary reef. The greater southerly extent (to 33°S, at Margaret River; Playford, 1997) and more vigorous development of last interglacial reef is considered to represent a stronger Leeuwin Current at that time.

The Holocene transgression in the Ningaloo reef tract reached a height of +1 m some 4000 years ago, (Wyrwoll et al., 1993) compared to the last interglacial high stand of +4 m. The Holocene reef crest grew along the seaward margin of the last interglacial reef system, so its vertical growth potential was limited by the elevation of the reef system it colonized.

### Reefs of the Pilbara coast

Reef systems in this region are the Dampier Archipelago, close to the coast, and offshore island-associated reefs at the Montebello and Barrow Islands. The Dampier Archipelago is high in coral diversity but is subject to extreme environmental conditions such as macro-tides, cyclones and storms as well as fluctuating turbidity and warming temperatures in an area of growing industrialization.

The offshore islands form a complex archipelago of over 250 small islands with a mainly tropical flora and fauna.

### Reefs of the Kimberley coast

Reefs along the Kimberley coast and shelf lie within a major hydrocarbon province and are essentially of two types; isolated offshore reefs and fringing reefs. Along the deeply embayed, macrotidal Kimberley coast is an extensive chain of fringing reefs which are very poorly known, but there are indications that they are of international significance and are in need of intensive study (Wilkinson, 2008). The most significant offshore reefs are the Rowley Shoals, and Scott Reef. These reefs and small carbonate platforms formed along an old Miocene continental margin; during the Miocene the Scott Reef/Rowley Shoals platform formed a narrow continental shelf, and the reefs have persisted there despite rapid subsidence of the shelf edge since the mid-Miocene. Whilst the offshore reefs are subject to cyclones and bleaching (Smith et al., 2008; Heyward et al., 1997) due to their isolated position some of the reefs are regarded as amongst the most pristine environments remaining in the world (Wilkinson, 2008).

The Rowley Shoals (Mermaid, Clerke and Imperieuse Reefs) were described as the most perfect morphological examples of shelf atolls in Australian waters (Fairbridge, 1950). The three shoals have similar dimensions, shape, orientation and distance apart, and all rise from the distal ramp of the North West Shelf at latitudes 15–17°S. From northeast to southwest the reefs rise from progressively shallower depths on their landward sides; Mermaid Reef from 440 m, Clerke Reef from 390 m, and Imperieuse Reef from 230 m. Each atoll (length range 15–17 m, width range 7–9 km) has north-south orientation, is pear-shaped with the narrower end to the north, and has a reef which encloses a single central lagoon which is ovoid and relatively deep in Mermaid Reef, but becomes increasingly shallow and segmented in Clerke and Imperieuse Reefs. About two thirds of the way up its eastern side, each system has a narrow passage (or passages), through which tidal flushing and sediment exchange occur.

Mermaid Reef has, on its western side, an outer reef flat (0.5 km wide), which is exposed at low tide, and a back reef of similar width, backed by 1 km wide sand flat. The eastern reef is only 0.6 km wide and the sand flat is absent. The western outer reef slope has well-developed spur and groove, the outer reef has coralline algae and slow-growing corals, while the back reef flat has a cover of living and dead coral and algal turf (Berry and Marsh, 1986). At Clerke Reef the shallow (<10 m) lagoon is segmented into three parts by sand sheet development. Imperieuse Reef has a lagoon partitioned into three basins by sand sheet development but the two along the eastern edge are deeper than the larger, central basin which is extensively infilled by a meshwork of coral growth, composed of flat-topped coalescent reef with intervening sand-floored depressions. The coral assemblages described for



Scott Reef by Done et al. (1994) are also recorded at Rowley Shoals. Differences in reef morphology, hydrodynamic exposure and ponding are reflected in the assemblages. Seismic studies indicate Holocene reef thicknesses of 18–36 m based on the difference in the depth of the last interglacial reflector in the lagoon (36 m below sea level in Mermaid Reef, but only 18 m below sea level in Imperieuse Reef; Collins, 2009) suggesting that differential tectonic subsidence since the last interglacial has controlled the accommodation space available for Holocene lagoon infill, which at Imperieuse Reef was only 50% of that available at Mermaid Reef, and this is an important control on the differential amounts of lagoon infill observed between the two reefs.

### Reefs and shoals of the Sahul Shelf, Northern Australia

Marginal to the Sahul Shelf and close to the Timor are a series of isolated reefs (Seringapatam, Ashmore Reef; Cartier Island) and shoals (Karmt, Big Bank and Echo Shoals; Heyward et al., 1997). The shoals formed a string of islands seaward of the palaeo-coastline and were drowned in the last 20,000 years (Lavering, 1993) becoming submerged to below the euphotic zone, terminating carbonate production by photosynthetic organisms. Thereafter bank growth has been by *Halimeda* accumulation, which has apparently dominated since the Late Pleistocene (Heyward et al., 1997).

### Summary

Coral reefs in Western Australia are rich in marine biodiversity, and are ranked second in the world in terms of endemism (Wilkinson, 2008). Whilst industrial impacts will increase in the future, reefs in this vast area are usually far from population centers. Though some are close to the coast, there is low terrestrial runoff because of the dry and arid climate. Whilst there are challenges for research, monitoring and management due to remoteness and the vast distances involved, research and management planning are increasing commensurate with international recognition of the region's importance.

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## Cross-references

Barrier Reef (Ribbon Reef)  
 Climate Change and Coral Reefs  
 Coral Reef, Definition  
 Fringing Reefs  
 General Evolution of Carbonate Reefs  
 Indian Ocean Reefs

## WESTERN INDIAN OCEAN

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## Definition

The Western Indian Ocean is defined as the tropical region bounded by the Gulf of Aden on the north, by eastern Africa on the west, by the Chagos and Maldivé Archipelagoes on the east and by latitude 26°S on the south. The ocean washes the African coasts from Somalia to south Mozambique, Madagascar and a myriad of high- and low-lying islands, in particular, the Seychelles.

## Reef sites

The coral reef areas in the Western Indian Ocean (WIO) are latitudinally distributed between about 2°N and 26°S. The southernmost coral communities that grow along the South African coasts at 27°50'S are not regarded as true coral reefs.

Fringing reefs are widespread, especially along the eastern African coasts from Somalia, Kenya, Tanzania to Mozambique, around the granitic Seychelles Islands (Mahé, Praslin), the Mascarene (Réunion, Mauritius, Rodrigues) and the Comoro Islands and on the northwestern sides of Madagascar. Barrier-like structures are restricted to Rodrigues and Mayotte Islands, the southeastern coast of Mauritius, northwestern and southwestern coasts of Madagascar. Atolls and/or low-lying coral islands (reef platforms) form the carbonate Seychelles (e.g., Aldabra, the Amirantes

and Farquhar Islands), Agalega Islands and most of the so-called French Scattered Islands (Tromelin, Europa, Juan de Nova, Bassas da India). Partly to totally submerged bank reefs include Soudan, Glorieuses, Cargados Carajos (Saint Brandon), Nazareth and Saya de Malha, located north to northeast of Madagascar and Mauritius. Except for Madagascar and the granitic Seychelles regarded as continental remains, the core of all these islands is likely to be volcanic in origin (Stoddart, 1971). Most of the data on the WOI reef attributes were gained from the fringing and barrier systems. Little is known about atolls, reef platforms and bank reefs.

## Main attributes of reef communities

The WIO has a high generic coral diversity. The number of genera is the highest in the Seychelles areas (>50) and decreases with increasing latitude as a response to decreasing sea surface temperature. This number ranges between 30 and 35 at the southern most part of Mozambique (about 24°S) and at the entrance of the Gulf of Aden (about 12°30'N). Four major groups of coral assemblages have been identified according to changes in wave exposure, light level and depth (Faure, 1982).

Group I refer to coral assemblages living along the deeper fore-reef zone at depths greater than 30 m. These assemblages are dominated by the encrusting *Echinophyllia* and *Leptoseris*. Group II include the communities inhabiting the intermediate and upper fore-reef zones. The intermediate parts (<30 to about 10–15 m) are composed usually of encrusting or foliaceous forms including *Pachyseris*, *Echinopora*, *Cyphastrea*, *Turbinaria*, *Montipora* and a variety of massive faviids (*Favia stelligera*, *Favites halicora*). The upper parts of outer slopes (<10 m) are usually made up of tabulate corals (*Acropora hyacinthus* group; *Acropora tenuis*), massive *Porites* replaced upwards by robust branching corals (mostly *Acropora robusta* or *A. humilis* groups; *Pocillopora verrucosa* and *P. eydouxi* groups; *Stylophora*) and the hydrocoral *Millepora platyphylla*.

Group III is typified by reef-crest and reef-flat coral communities. At high water-energy settings, reef-crest and outer reef-flat zones dominantly exhibit those robust acroporid forms colonizing the uppermost fore-reef slopes, together with *Montipora tuberculosa*, *Acropora mammilata* and massive faviids (*Favites melicerum*, *Favia stelligera*). In less agitated areas, corals mainly include arborescent branching *Acropora muricata*, *A. hemprichi*, gracile *A. variabilis*, *Galaxea fascicularis* associated with domal *Porites lutea*, and *Montastraea curta*. In inner reef-flat zones, the prominent corals are arborescent *Acropora muricata*, *A. palifera*, *A. pulchra*, tabulate *A. cytherea*, with *Pocillopora damicornis*, *Pavona divaricata*, *Porites solida*, *P. nigrescens*, *P. andrewsi*, *Synarea iwayamaensis* and *Goniastrea retiformis*.

Group IV refers to coral communities inhabiting backreef and lagoonal environments. These are dominated

by forms adapted to low water energy conditions and represented by *Acropora muricata*, *A. hyacinthus* group, *Pavona danai*, *P. divaricata*, *P. varians*, *Porites lutea*, *P. solida*, *Synarea iwayamaensis*, *Goniastrea pectinata*, *Leptastrea purpurea* and *Lobophyllia corymbosa*.

Most reefs possess non-elevated coralline algal pavements. Typical algal ridges locally with an elevation of about 1 m, have been described from Rodrigues, Caragos Cargados Banks and the granitic Seychelles. The development of these structures within the region is regarded as controlled by the intensity of southeast trade winds (Rees et al., 2005).

### Sediment components and carbonate production

The major compositional characteristics of surficial sediment assemblages from the WIO reefs can be summarized as follows (Montaggioni and Braithwaite, 2009).

In most fringing reefs, a basic distinction can be made between and within the different environments in terms of the coral content. The fore-reef sites contain highly variable amounts of coral particles (2 to about 50% of the total sediment). By contrast, reef flats and proximal back-reef settings have coral contents not lower than 20% and approximating to 60%. These values partially reflect the high cover rates of coral assemblages (30–80%). On barrier reefs and atolls, there is a distinct separation between outer reef rims and lagoonal environments in terms of coral composition. In most lagoonal sheets of both barriers and atolls as in Mayotte, coral is a secondary component, forming 3 to less than 15% of detritus on an average. The scarcity of coral detritus clearly is indicative of local impoverishment in coral coverage (less than 10% of the substrate) except in portions adjacent to patch reefs and coral buildups with high coral coverage. Similar to corals, coralline algae generally exhibit higher abundance in sediments deposited close to reef margins and coral patches. Irrespective of reef types, the amount of coralline fragments was found averaging 5–15 to 30% of the total sediment, from deeper fore-reef to back-reef zones as observed in Réunion, Mauritius, Rodrigues and Mahé Islands. By contrast, lagoonal environments generally exhibit low concentrations in corallines, averaging 0 to around 4% of the sediments on most barriers and atolls. Debris from green algae *Halimeda* vary considerably in abundance throughout the region. Their amount ranges between 0% and 90% of the total sediment, reaching the highest values in the granitic Seychelles and are absent from high-latitude reefs of southern Mozambique. The proportions of molluscan bioclasts average 10–25% of the carbonate material along the fore-reef slopes and in the reef-flat environments. In back-reef and lagoonal settings, molluscs increase markedly in abundance (25–45%). In many reefs, benthonic foraminiferal detritus dominates along the fore-reef slope, representing 17 to approximately 60% of the total sediment grains. By contrast, their amount declines markedly in reef-flat, back-reef zones, and lagoons not exceeding 2–20% in all studied sites.

Estimates of calcium carbonate regionally deposited by oceanic island reefs over the last 5,000 years are approximately 217 Gt, expressing a flux of  $4.3 \times 10^{11}$  mol yr<sup>-1</sup> CaCO<sub>3</sub> into sediments. Assuming that each mole of CaCO<sub>3</sub> releases 0.6 mol of CO<sub>2</sub> to the atmosphere, about  $2.6 \times 10^{11}$  mol yr<sup>-1</sup> CO<sub>2</sub> are estimated to have been transferred by WIO reefs to the atmosphere during the optimal phase of reef growth (9,000–4,000 years ago), representing 57 Gt CO<sub>2</sub>. These values do not include carbonate production in the early and late Holocene and contributions from eastern Africa and submerged bank reefs. As such, the volumes of CaCO<sub>3</sub> accumulated and CO<sub>2</sub> released by the whole WIO reefs may effectively be doubled (Rees et al., 2005).

### Reef growth history during the last deglaciation

A detailed regional reconstruction of reef growth history in relation to the rise in sea level over the last 18,000 years has been provided based on reef coring (Réunion, Mauritius, southwestern Madagascar, Mahé, Mayotte), submersible observations and sampling of fore-reef slopes at Mayotte (Camoin et al., 2004).

An earlier fringing reef generation developed at around 20,000–18,000 years BP along the Mayotte foreslopes when sea level was about 110–120 m below its present position. A second reef tract dated at 13,600 years BP occurs at a present water depth of 90 m. It was drowned at 13,500 years BP (Meltwater Pulse 1A). A third reef generation at present submerged at 60 m depth is regarded as formed at around 12,000 years BP. However, there is no direct evidence to support a well-defined surge at about 11,500 years BP (Meltwater 1B). Throughout the region, modern reefs appear to have started to grow between 9,000 and 8,000 years BP. Rates of vertical reef accretion range between 0.9 mm yr<sup>-1</sup> and 7 mm yr<sup>-1</sup>. The reconstructed sea-level curves reflect a rapid rise in sea level at about 6 mm yr<sup>-1</sup> from 10,000 to 7,500 years BP, followed by a marked slowing to 1.1 mm yr<sup>-1</sup>. Sea level reached its present position by 3,000–2,500 years BP.

### Emerged reefs and related features

Numerical predictions assume that there should be a mid-Holocene high stand around 5,500 years BP in the WIO. However, the only robust evidence for mid to late Holocene higher sea-levels to date comes from 2,000 to 3,700 year-old coral and vermetid encrustations at heights of +0.30 to +2.50 m around Madagascar. The lack of Holocene higher sea stand in the volcanic and low-lying carbonate islands and the granitic Seychelles results probably from the negligible effects of glacial isostatic adjustment (hydro-isostasy) on these areas or from compensation by other mechanisms, in particular active subsidence of volcanic aprons (Camoin et al., 2004).

By contrast, reef remains of Late Pleistocene high sea stands, dated at approximately 120,000 years BP (Marine Isotope Stage 5 e) and locally at 240,000 years



BP (Stage 7) are widely distributed along eastern African coasts (Kenya, Tanzania), Mauritius, Madagascar, Europa, Glorieuses, the granitic Seychelles, Aldabra and nearby islands including Assumption, Astove, Cosmoledo and St. Pierre (Stoddart, 1984). The highest elevation of Stage 5 e-reef terraces above the present sea level ranges between about 10–12 m (Kenya), 5–6 m (Tanzania, Madagascar), up to 8 m (the Seychelles Island Groups) and less than 2–3 m (Mauritius, Europa, Glorieuses), thus reflecting differential geodynamic behaviors.

### Coral paleoclimatology

Several reconstructions of the regional climate variability based on geochemistry of massive *Porites* were presented spanning the last three centuries. In particular, contrary to the global warming trend, the Seychelles record reveal a monsoon-driven cooling of the Western equatorial Indian Ocean since the middle of the nineteenth century (Pfeiffer and Dullo, 2006).

### Summary

The WIO exhibits a great variety of reef types surrounding continental masses and high- and low-lying islands. It is typified by a high coral generic diversity (30 to >50). The genera *Acropora*, *Pocillopora* and *Porites* are the major reef builders irrespective of reef site, while the development of coralline algal ridges remains relatively limited. The modern reefs are likely to have begun to develop regionally from about 9,000 years BP. Over the past 5,000 years, their calcium carbonate production is estimated to have been higher than  $400 \times 10^9$  tons. There is little evidence of Holocene reef remains at elevations higher than present sea level. By contrast, reef terraces

deposited during MIS 7 and 5 e high sea stands are at present exposed in a number of sites throughout the region.

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### Cross-references

[Climate Change: Impact of Sea Level Rise on Reef Flat Zonation and Productivity](#)  
[Eastern Indian Ocean – Northern Sector](#)  
[Emergent Reefs](#)  
[Glacio-Hydro Isostasy](#)  
[Indian Ocean Reefs](#)  
[Last Interglacial and Reef Development](#)  
[Paleoclimate from Corals](#)

# Y

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## YONGE, SIR MAURICE (1899–1986)

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### Definition

An eminent British zoologist, who led the 1928–1929 Great Barrier Reef Expedition to Low Isles and who, together with other team members, provided some of the earliest insights into the feeding biology, growth and reproduction of reef corals. He was also one of the first scientists to describe the bleaching of corals under natural conditions and to investigate the bleaching process both in manipulative experiments and in the field.

Maurice Yonge was an extremely distinguished marine zoologist whose research interests spanned both molluscan and coral physiology. He completed an undergraduate and postgraduate degree at the University of Edinburgh before beginning postdoctoral research at Plymouth Marine Laboratory on feeding and digestion in bivalves. In 1927 he accepted the leadership of the Great Barrier Reef Expedition and soon after began to assemble his interdisciplinary team for a 13 month stay on Low Isles in the northern Great Barrier Reef. The expedition members were divided into a boat party, a shore party and a physiological party with a geographical party also operating alongside the other activities. The 1928–1929 expedition marked the beginning of modern coral reef science with research focussed on *in situ* relationships between reef growth and environment. The biological outputs provided novel information on coral nutrition, growth and

reproduction and early observations and experimental accounts of coral bleaching while the geographical party produced detailed reef surface mapping at a level which had not been previously achieved.

One of the main conclusions arising from the expedition on experimental work with corals was that they were superbly efficient and voracious carnivores and that their symbiotic zooxanthellae made no significant contribution to their nutrition. Much later, in 1964, Yonge began a collaboration with Thomas and Nora Goreau in which they showed, using autoradiography, the importance of zooxanthellae in the nutrition of the giant clam, *Tridacna*. They later acknowledged that corals too might also benefit from the passage of material from the zooxanthellae to the tissues of the animal host, a fact which had by 1970 been established by a number of other scientists.

Although Maurice Yonge's major interests focussed on the bivalve Mollusca his contributions to coral reef science were highly significant with his papers still being cited by authors today, some 80 years after the initial expedition. He was elected to the Fellowship of the Royal Society of London in 1946 and received the Darwin Medal of the Royal Society in 1968 for his work on the evolution of the Bivalvia. He was knighted in 1968 for his contribution to marine science over a 60 year period of active research and service to the subject.

### Cross-reference

[Royal Society of London](#)  
[Steers, James Alfred \(1899–1987\)](#)  
[Stoddart, David Ross \(1937–\)](#)

# Z

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## ZOOXANTHELLAE

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### Synonyms

Algal symbionts; *Symbiodinium*

### Definition

The term “zooxanthellae” refers to a paraphyletic group of yellow-brown microalgae, including certain dinoflagellates, diatoms, cryptophytes, chrysophytes (golden algae), and rhodophytes (red algae), that are found in mutualistic symbiosis with a variety of invertebrate and protist hosts. “Zooxanthellae” is a plural noun (singular: zooxanthella) derived from the Greek words *zoo* (animal), *xanthos* (yellow), and *ella* (diminutive): “yellow animal cells.” On coral reefs, vernacular usage almost exclusively refers to the symbiotic dinoflagellates in the genus *Symbiodinium* that are commonly found in certain corals, anemones, jellies, clams, worms, sponges, and other reef organisms.

### Introduction

Zooxanthellae are ubiquitous and critical members of coral reef ecosystems (Taylor, 1974; Muscatine and Porter, 1977; Trench, 1993; Rowan, 1998). They are normally abundant, with healthy reefs typically containing  $>10^9$  cells per  $m^2$ , but due to their small size (10  $\mu m$  diameter) their overall biomass on reefs is low. Because they are so important to the construction, evolution, and ecology of coral reefs, zooxanthellae can be regarded as keystone species on coral reefs – perhaps the only protists to play such a role.

Zooxanthellae provide significant nutritional benefits to their hosts in the form of translocated photosynthates, particularly glycerol and other water soluble compounds

such as glucose. In a variety of scleractinian corals, photosynthates from dinoflagellate zooxanthellae (in the genus *Symbiodinium*) have been shown to account for 50–95% of the coral’s energy budgets. In addition, the presence of algal symbionts drives rapid calcification in the host organism, and allows scleractinian corals to accrete limestone skeletons, dominate as the principal builders of contemporary reefs, and compete for space in the shallow tropical seas where they are most commonly found.

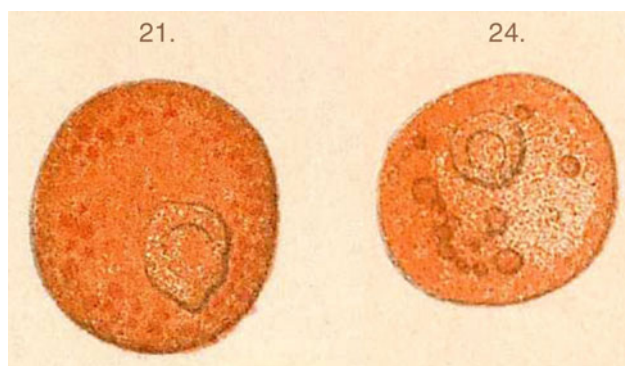
Recently, coral–algal symbioses have become a major focus of research inquiry as a result of coral reef “bleaching,” in which reef corals and other zooxanthellate hosts lose their algal symbionts (or experience a reduction in their per-cell pigment concentrations) and become pale or white as the calcium carbonate skeleton becomes increasingly visible through the translucent coral tissue. In some cases, residual coral pigments result in bleached corals appearing pale blue, pink, yellow, purple, chartreuse or other colors, rather than the typical white appearance.

Bleaching events are becoming increasingly frequent as a result of rising sea surface temperatures, and have been responsible for widespread coral mortality in some reef regions (Hoegh-Guldberg et al., 2007). Moreover, with ocean acidification resulting in declining rates of coral calcification, the role of algal symbionts in influencing the response of their calcifying hosts appears poised to be a similarly active research field.

### Diversity and distribution of zooxanthellae

In 1883, Karl Brandt first recognized that the “animal chlorophylls” he studied in radiolarians were, in fact, mutualistic algae (Figure 1). He introduced a new genus *Zooxanthella* to refer to these algae, but this name was quickly dropped, as the phylogenetic diversity of these algae (see Definition) became apparent.





**Zooxanthellae, Figure 1** Original drawings of “zooxanthellae” reproduced from Brandt (1883). Shown are the *Gelbe Zellen* (“yellow cells”) isolated from the scleractinian coral *Cladocora caespitosa* (“21”) and the upside-down jellyfish *Cassiopeia borbonica* (“24”). Both are *Symbiodinium* based on their appearance and host origin.

The first dinoflagellate zooxanthellae were cultured in the 1950s, and in 1962 Hugo Freudenthal introduced a new genus and species *Symbiodinium microadriaticum*, from the Greek words *symbion* (“living together”) and *dinos* (“whirling”), to describe the gymnodinioid dinoflagellates isolated from the upside-down jellyfish *Cassiopeia xamachana* (Freudenthal, 1962). Because no further species in the genus were formally described for several decades (with eight species names eventually validated by formal description in 2000), it was generally assumed that all symbiotic dinoflagellates belonged to a single pandemic species *S. microadriaticum*, despite the fact that evidence pointing to significant diversity within the genus had begun to accumulate since the 1970s.

In fact, there are currently eight genera in four or five orders of dinoflagellate that are recognized as endosymbiotic zooxanthellae in marine invertebrates and protists (Banaszak et al., 1993; Trench, 1997). *Symbiodinium* is the most studied genus in this paraphyletic group and is commonly found in shallow water tropical and subtropical cnidarians. Cnidarian species reported to contain *Symbiodinium* include many representatives from the class Anthozoa (including anemones, scleractinian corals, black corals, zoanthids, corallimorphs, blue corals, alcyonacean corals, and sea fans) and several representatives from the classes Scyphozoa (including rhizostome and coronate jellyfish) and Hydrozoa (including milleporine fire corals). *Symbiodinium* has also been identified from gastropod and bivalve mollusks (including tridacnid [giant] clams, heart cockles, and conch), large miliolid foraminifera (in the subfamily Soritinae), sponges, and a giant heterotrich ciliate (see Trench, 1993; Baker, 2003 for review). Some records of “zooxanthellae” present in invertebrates and other hosts have been based on observations of just a handful of individuals, or are based on only cursory observations or anecdotal reports. Because systematic surveys of potential hosts have not been undertaken, it is likely that additional

zooxanthellate hosts exist in nature which have yet to be reported.

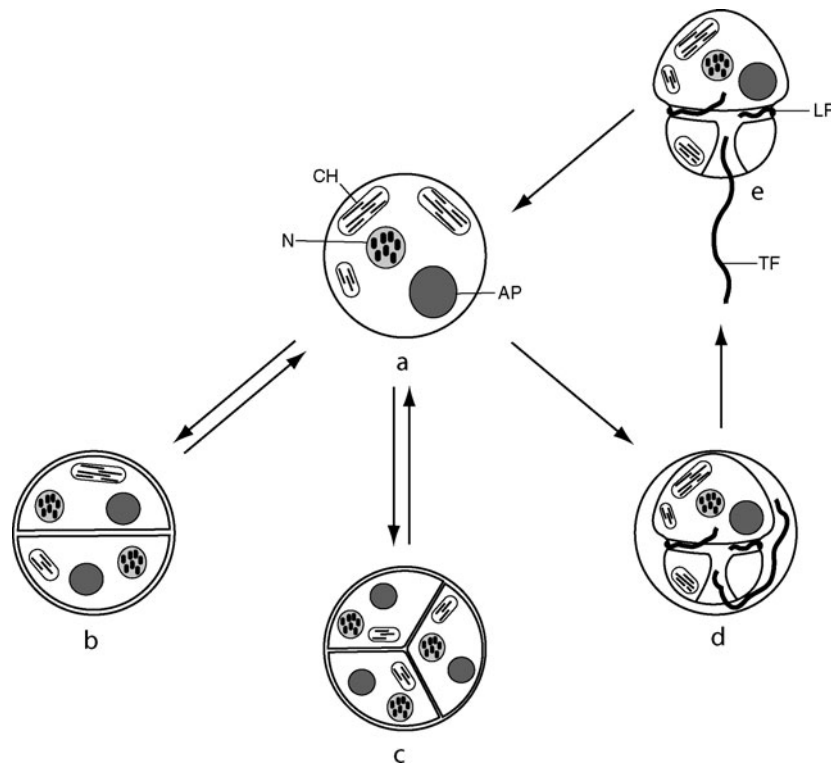
Although zooxanthellae can be found in a wide variety of hosts, algal symbiosis tends not to be the norm for any particular taxonomic group. For example, while scleractinian corals are the principal builders of contemporary coral reefs, the majority of species in the order Scleractinia are in fact deep water and azooxanthellate. Moreover, some individual species are facultatively zooxanthellate, able to survive indefinitely in both a symbiotic and non-symbiotic state, depending on environmental conditions (e.g., certain species in the scleractinian coral genus *Oculina*, which is zooxanthellate in shallow water, but azooxanthellate at depth). Together, these patterns indicate that symbiosis with algae has evolved independently multiple times, even within individual groups such as anthozoans.

The life cycle of *Symbiodinium* alternates between a vegetative cyst and a motile zoospore (Figure 2), with the vegetative stage being the dominant form in endosymbiosis. Relatively little is known of the diversity and ecology of free-living *Symbiodinium*, although they are now routinely identified in reef waters and/or sediments (Carlos et al., 1999; Gou et al., 2003; Lewis and Coffroth, 2004; Coffroth et al., 2006; Littman et al., 2008; Manning and Gates, 2008; Porto et al., 2008). It is not yet clear how much *Symbiodinium* diversity exists in these free-living pools, and what overlap and/or interactions exist between these algae and those in endosymbiosis. This is currently an active area of research.

### Diversity and flexibility in coral–algal symbiosis

The dinoflagellate genus *Symbiodinium* is extraordinarily diverse, and consists of at least eight major clades (A–H, Santos and Coffroth and Santos, 2005; Pochon et al., 2006). Members of five of these clades (A, B, C, D, and F) have to date been documented in scleractinian corals. It is clear that additional diversity in *Symbiodinium* remains to be discovered, and that most species are uncultured and undescribed (Rowan, 1998; Santos et al., 2001). Moreover, in addition to the dominant populations of symbiotic dinoflagellates in these hosts, many unusual or novel variants may also occur as cryptic and unstable transients whose physiological or ecological importance is not yet clear (LaJeunesse, 2001; Santos et al., 2001; Toller et al., 2001). It is likely that additional diversity (at both the clade level and the subclade level) will be discovered with increased sampling of understudied zooxanthellate hosts, such as forams, anemones, sponges, and octocorals.

Scleractinian corals often show flexibility in the types of *Symbiodinium* they can host, both within and among clades (Baker, 2003). Although one symbiont type is usually dominant in any given coral species and environment (Rowan and Powers, 1991; LaJeunesse, 2002; LaJeunesse et al., 2003), the ability of some corals to host different symbionts in different environments or locations suggests



**Zooxanthellae, Figure 2** Life cycle of *Symbiodinium* (a) vegetative cyst, (b) dividing vegetative cyst producing two daughter cells, (c) dividing vegetative cyst producing three daughter cells, (d) developing zoospore, and (e) zoospore. CH: chloroplast; N: nucleus; AP: accumulation product; LF: longitudinal flagella; TF: transverse flagella. (Adapted from Schoenberg and Trench [1980] and Freudenthal [1962], and reproduced with permission from Stat et al. [2006].)

that these corals may possess different physiological optima depending on the algal symbiont(s) they host. Moreover, because these corals appear able to change the dominant symbiont type in response to environmental changes (Rowan et al., 1997; Rowan, 1998; Baker, 2001, 2003; Little et al., 2004; Berkelmans and Van Oppen, 2006; Jones et al., 2008; LaJeunesse et al., 2009), it has been suggested that flexibility in coral–algal symbiosis is an important mechanism by which reef corals adapt or acclimatize to disturbances, including those resulting from climate change (Buddemeier and Fautin, 1993; Baker, 2001, 2003; Baker et al., 2004; Berkelmans and Van Oppen, 2006). Although evidence exists in support of these hypotheses, the large-scale implications for coral reef survival through the coming century have yet to be established (Hoegh-Guldberg et al., 2007). In addition, there are likely to be trade-offs between different symbiont types (Little et al., 2004) that have yet to be explored in detail. Diversity and flexibility in coral–algal symbiosis remain an active area of research for exactly these reasons.

## Summary

The endosymbiosis between scleractinian (stony) corals and zooxanthellae (typically symbiotic dinoflagellates in the genus *Symbiodinium*) underpins the success of modern

coral reefs. Reef corals (and other contemporary reef-builders) gain a twofold advantage by hosting zooxanthellae. First, they can function as autotrophs and use the photosynthates thus obtained as an energy substrate. Second, for reasons which remain unclear, they are able to calcify much faster than their azooxanthellate counterparts (Cohen and McConnaughey, 2003). Together these phenomena explain why coral reefs have become dominant ecosystems in shallow, oligotrophic tropical seas. They also explain why coral reef bleaching (the loss of zooxanthellae from reef-builders) as a result of environmental stress is a major threat to coral reef ecosystems, particularly as a result of climate change-related seawater warming. The potential role of zooxanthellae in mediating the response of reef builders to ocean acidification also illustrates their importance as a contemporary subject of research.

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[Ocean Acidification, Effects on Calcification Symbiosis](#)  
[Temperature Change: Bleaching](#)



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